AN INVESTIGATION INTO DIFFERENT SAMPLING TECHNIQUES AND GEOGRAPHIC VARIATION IN SIZE-FECUNDITY PARAMETERS OF THE AMERICAN LOBSTER, *H. americanus*

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An investigation into different sampling techniques and geographic variation in size-fecundity parameters of the American lobster, *H. americanus*

by

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Abstract

This thesis focuses on two main aspects, the first of which looks at non-invasive sampling techniques to estimate fecundity and the second looks at a model that can predict size-fecundity parameters from latitude. The non-invasive sampling techniques estimate fecundity for ovigerous American lobster (*Homarus americanus*) based on measurements and digital image analysis. Non-invasive fecundity estimates can now be made that require the removal of only ten eggs per female. Applications of this technique includes the evaluation of the efficacy of conservation measures, such as v-notching or the establishment of closed areas, aimed at increasing egg production, where differences in egg production can be quantified without the use of destructive sampling techniques. In order to create a model able to predict size-fecundity relationships throughout the species range, fecundity estimates for American lobster (*H. americanus*) from 11 different locations in the Northwest Atlantic (from the Strait of Belle Isle, Newfoundland to Buzzards Bay, Massachusetts) were obtained. The data were then analyzed for geographic variation and a latitudinal gradient was found in the size-fecundity parameter *b*. This was then used to create a model that can predict size-fecundity relationships from latitude. This model will allow for future fecundity estimates to be made, utilizing size data from latitude for any population in the Northwest Atlantic.

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CHAPTER 1

1.0 Overview

Crustaceans are one of the largest groups within the animal kingdom, and there has been growing interest in their theoretical and applied biology. This is attributed not only to their commercial importance, but also to various characteristics that make them an ideal study species for physiological, biochemical, and neurobiological research (Mente and Neofitou, 2008). These characteristics include longevity, convenient size, wide distribution, and ease of availability (Mente and Neofitou, 2008).

In addition to the interest in crustacean's theoretical and applied biology, research has focused on egg production or fecundity, especially in commercially valuable species and/or species inhabiting specialized or unique environments (Wenner and Kuris, 1991). For example, successful spawning in Fiddler crabs is controlled by sporadic rainfall (Costa and Negreiros-Fransozo, 2002) and crayfish develop unusual egg production patterns in habitats considered "non-typical" for crustaceans (Huner and Lindqvist, 1991). Moreover, species with economic importance such as the crayfish and lobster have been the focus of various types of research. Within the *Jasus* genus, research has focused on factors influencing fecundity and population egg production in seven different species (Annala, 1991), while egg size was the focus of a study that looked at 52 different species within the superfamily Galatheoidea (Dover and Williams, 1991).

Evolutionary pressure and resulting adaptive processes, to increase survival of offspring, has lead to a large variety in the reproductive patterns of crustaceans (Hartnoll and Gould, 1988). To aid in the successful management of various crustacean fisheries, knowledge on the reproductive biology in relation to growth patterns, as well as size at sexual maturity and

fecundity are of great importance (Kennelly and Watkins, 1994). However, traditional models, such as growth models, which are applicable to fish, cannot be directly applied to crustaceans because fish are characterized by continuous growth, whereas crustaceans display discontinuous growth (Lizarraga-Cubedo *et al.*, 2008). However, research on growth in crustaceans is incorporated into models that aid in the enumeration of egg counts within females (Paul and Paul, 2000). Within the crustacean fisheries, the incidence and presence of berried females, is an important parameter used to determine the size at first maturity.

In female crustaceans, reproduction is dependent upon the number of individuals within a size class, size at maturity, fecundity, and frequency of spawning (MacDiarmid, 1989; Tulley *et al.*, 2001). Reproduction in male crustaceans is only limited by mate availability, not sperm (MacDiarmid, 1989). Throughout the incubation period, female lobster can lose up to 37 % of their eggs depending on various factors (Perkin, 1971). Fecundity can be estimated using different methods. Potential fecundity is described as the number of oocytes in mature ovaries, actual or real fecundity refers to the number of eggs attached to the pleopods at time of capture, and effective or realized fecundity estimates the number of eggs attached to the pleopods of gravid females at time of hatching (Mente, 2008). Fecundity used in the study refers to actual or real fecundity, which is important in the perspective of stock-recruitment.

Comparisons of fecundity among different species of lobsters have shown that clawed lobsters have a relatively low fecundity (Cobb *et al.*, 1997), attributed to difference in reproductive strategies and longer protracted larval periods (Polluck, 1997). For example, spiny lobsters (no claws) are considered highly fecund, having smaller egg sizes and hatched larvae require several moults before settling to the bottom. This is in contrast to the American lobster

(clawed) that has large eggs and the larvae settle to the bottom in only three moults (Polluck, 1997).

The positive relationship between crustacean fecundity, which refers to the total number of eggs an ovigerous female carries externally, and size has long been known (Tack, 1941; Forster, 1951; Jensen, 1958). Models range from simple linear regressions to complex asymptotic curves (Somers, 1991). This complexity, and the observed variability in crustacean fecundity, makes a general description of their reproductive biology difficult (Klaoudatos and Klaoudatos, 2008). A combination of this complexity and the concerns with overfishing recruits has lead to stronger regulations and a shift from general crustacean models to species specific models (Caddy, 1977, 1979; Ennis and Akenhead, 1978). The incorporation of reproduction into species-orientated models and the effects that harvest policies have on egg production were not introduced until the 1980's (Botsford, 1991) largely due to limited data. Species oriented models are now used in stock assessments to evaluate the effects harvest policies and conservation measures have on populations. The stock-recruitment relationship usually represents stocks in terms of egg production, and describes the reasonable assumption that at low levels of egg production there will be low numbers of recruits, and increases in egg production will proportionally increase the number of recruits (Botsford, 1991).

There has been extensive research on the size-fecundity relationships of *H. americanus*, which is one of the many parameters used in the construction of life history and length structured models to evaluate the efficacy of various conservation measures, such as minimum and maximum legal size (Atlantic States Marine Fisheries Commission (ASMFC), 2009). Fecundity estimates are also used in analysis of total egg production in a population and per recruit (Factor, 1995) The intent of this thesis is to develop a non-invasive sampling technique to estimate

fecundity as well as a general model that can predict size-fecundity relationships for the American lobster, *Homarus americanus*, to aid in the management of the species.

To date, studies that investigate the size-fecundity relationships of *H. americanus* have all required the removal of eggs from ovigerous females to obtain accurate fecundity estimates. This invasive technique is disliked because it removes eggs, potential recruits, from a population, and is also inconsistent with conservation measures that prevent the removal of eggs from females. The focus of Chapter 2 will be to describe new techniques that may provide accurate fecundity estimates, but do not require the complete removal of eggs from ovigerous females.

In some cases, as observed in the European lobster, *H. gammarus,* the size-fecundity relationships are similar throughout the species range (Tully *et al.*, 2001; Lizarraga-Cubedo *et al.*, 2003) and a simple relationship is applicable for the entire species. However, the size-fecundity relationships for *H. americanus* do not display uniformity among locations, and evidence for geographic variation has been stressed (e.g. Estrella and Cadrin, 1995). Latitudinal variation in lobster population parameters has been presented by Russell (1980), who hypothesized a north to south gradient in growth parameters based on a plot of the coefficients of the von Bertalanffy growth parameters. Similar results for size-fecundity parameters have not yet been shown, and geographic variation among these parameters has largely been dismissed because of the confounding affects of differences in collection and/or counting methods (Estrella and Cadrin, 1995), seasonal timing of study, sample size (Estrella and Cadrin, 1995; Ennis, 1981), inter annual temperature, environmental variables, and methods of collection (Estrella and Cadrin, 1995). This makes proper management of the species in regards to egg production and stock-recruitment difficult, since the size-fecundity relationship currently available are region specific and only applicable to the collection site. The lack of a general model that can predict

size-fecundity equations throughout the entire species range forces the need for future large-scale sampling. However, large-scale sampling is not easily accomplished as a result of increased value, regulation, and fishing effort for *H. americanus* (Estrella and Cadrin, 1995). A solution for this problem is discussed in Chapter 3, which provides a general model for formulating size-fecundity relationships for any location using latitude.

In many crustaceans, size-fecundity relationship is best described by a power function (MacDiarmid, 1989; Wooten, 1979) with exponents around 3, indicating that fecundity is a function of body mass (Mente 2008). The popularity of the power function (i.e. $Fec = aCL^b$) comes from its simplicity when both fecundity and female size are transformed into the logarithmic form (i.e. $\ln Fec = a + b\ln CL$), where Fec represents fecundity, CL represents carapace length, and a and b are the intercept and slope, of the relationship respectively (Somers, 1991). The method of log-transforming both fecundity and size allows for the linearization of data to facilitate graphical and statistical analysis (Smith, 1984; 1993), as well as transforming fecundity into a scale-independent measure, representing the proportional change in fecundity (Somers, 1991). Although the standard approach of a log transformation allows investigators to more readily compare results, it introduces biases (Packard, 2009; Smith, 1993; 1984) and may have negative consequences on the predictive power of the relationship (Zar, 1968, Smith 1980; 1984) Sprugel (1983) proposed a correction factor to eliminate the bias associated with log-transformed data and resulting allometric equations. Sprugel's correction factor was used by Estrella and Cardin (1995) to correct the fecundity estimates obtained from the log- transformed equations. Estrella and Cardin (1995) also suggested that future fecundity estimates undergoing logarithmic transformations would benefit from the use of Sprugel's correction factor. However, with the computer based graphics and sophisticated statistical software available today, virtually

any function can be fit to data without having to linearize the relationship. Therefore, the linearization of a relationship is no longer a sufficient rationale for making logarithmic transformations, and if transformations are not required then they should not be performed (Packard, 2009). A brief section in Chapter 3 will cover the bias associated with the fecundity equations obtained using logarithmic transformations.

The Canadian sea fisheries were valued at 1.6 billion dollars per year in 2008, with a third attributed to *H. americanus* (Department of Fisheries and Oceans (DFO), 2008). Furthermore, the fishery for *H. americanus* in Atlantic Canada and the United States has a combined average value of over one billion dollars per year (DFO, 2009; ASMFC, 2009). Therefore, it is particularly important to acquire a sound understanding of the size-fecundity relationships, in such a lucrative fishery, in order to aid in stock assessment, yield and egg per recruit models, and the proper management of *H. americanus*, by providing data on recruitment, fecundity, and stock viability. This thesis attempts to elucidate the size-fecundity relationship in *H. americanus*. Specifically my objectives are to: (1) develop a non-invasive sampling technique to accurately estimate fecundity in *H. americanus* that does not require the removal of eggs; (2) construct a general predictive model of size-fecundity relationships in *H. americanus* throughout its entire geographic range.

CHAPTER 2

A non-invasive sampling technique for estimating fecundity in the American lobster, *Homarus americanus*

2.1 Abstract

This study presents two non-invasive sampling techniques that estimate fecundity for ovigerous American lobster based on measurements and digital image analysis. These estimates are compared with fecundity estimates obtained from the widely used traditional invasive technique involving the removal, drying, and weighing of eggs. The results of these comparisons show that one non-invasive technique, which requires the removal of only ten eggs per female, is capable of producing fecundity estimates that vary little from those obtained using the traditional invasive method. Recent increases in conservation-oriented research makes this technique appealing for future work on the size-fecundity relationships, which are used in stock assessments and yield and egg per recruit models to aid in the evaluation of population biology for the American lobster.

2.2 Introduction

The fecundity of *Homarus americanus* is an important parameter, often used in life history, such as egg production per recruit and/or population, and length structured models to evaluate the efficacy of conservation measures and various biological reference points, such as maximum sustainable yield (ASMFC, 2009). There has been extensive research on the size-fecundity relationships of *H. americanus* for numerous locations throughout the species range. The earliest studies were carried out by Herrick (1896) in Massachusetts, which involved the collection and removal of over 4000 ovigerous females. More recent research has focused on coastal Newfoundland (Ennis, 1981) and the Canadian Maritimes (Campbell and Robinson, 1983). The most recent study, carried out by Estrella and Cadrin (1995), involved the collection and removal of over 400 ovigerous females from coastal Massachusetts. The ability to assess *H. americanus* fecundity in the field quickly, accurately, and without injury has proven difficult because current methodologies require physical removal and preservation of all eggs from females.

Female *H. americanus* are highly fecund, and can carry in excess of 80,000 eggs (Botsford, 1991), which precludes the enumeration of all eggs. Thus, fecundity estimations are usually made by counting the number of eggs in weighed subsamples and dividing the average weight of a single egg, as determined from the counted subsamples, into the weight of the entire egg mass (e.g. Ennis, 1981). Traditionally this involves removing, fixing, and drying of eggs, which makes this technique for estimating fecundity invasive and labour-intensive.

Non-invasive techniques such as sonography and endoscopy have been used to evaluate gender, gonad structure, and fecundity in some teleost fish populations (Bryan *et al.*, 2007). Alternate techniques, which have been borrowed or adapted from plankton biology (*e.g.*

Witthames and Greer Walker, 1987) have been used to automate the measuring of fecundity (Sailia *et al.,* 1961). Although these methods showed improvements in the accuracy of fecundity estimates, they still require substantial egg removal as well as special equipment, making it difficult to apply these methods in various types of research (Ganias *et al.*, 2008). Despite the detrimental effects of egg removal, fecundity estimates for *H. americanus* are still measured using the traditional invasive technique. This method requires the removal of all the eggs from a female, and results in an inconsistency among researchers, who destroy the eggs, and fishers, who must return berried females unharmed.

Recent increases in value, regulation, fishing effort, and conservation measures for *H. americanus* (Estrella and Cardin, 1995) prevents additional large scale sampling as carried out by Herrick (1896). The co-management of the species among fishers and scientists, limits the availability of permits that allow for the removal of eggs from a large number of females, and highlights the need for a reliable, non-invasive technique to estimate fecundity. This chapter focuses on non-invasive techniques that utilize measurements and digital image analysis to estimate fecundity in *H. americanus*. Fecundity estimates were made using two non-invasive techniques and compared to observed counts, determined using the traditional technique involving complete egg removal.

2.3 Materials and methods

2.3.1 Lobster collection

Ten ovigerous females ranging in size from 69-82 mm carapace length were collected using commercial lobster traps in May 2010 from various locations within Bonne Bay, Newfoundland (Fig. 1). It is thought that lobster size will have little impact on the estimation of egg number since the measurements are independent of carapace length. Fecundity estimates

were carried out using two non-invasive sampling techniques as well as the traditional invasive technique.

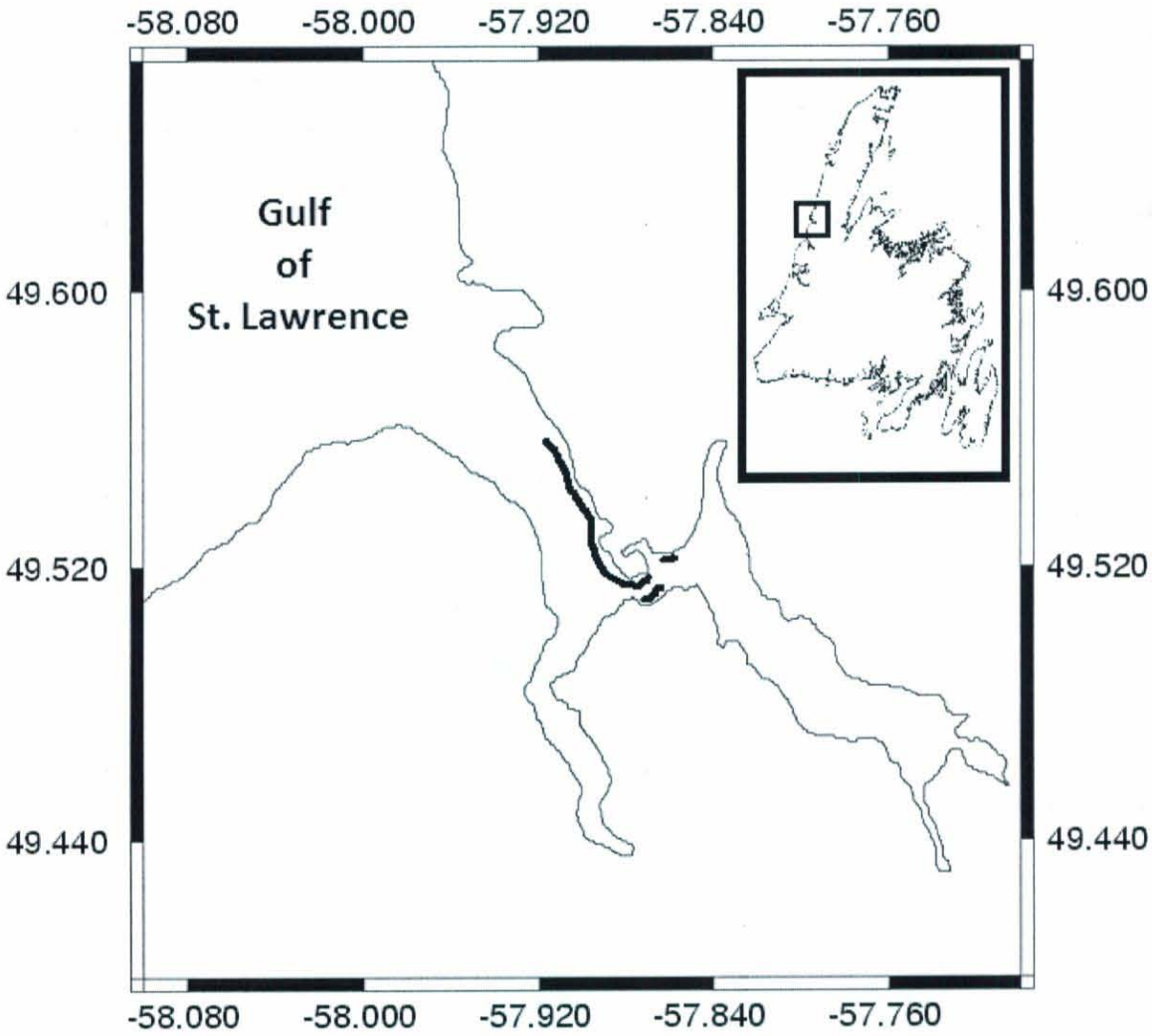

Figure 1. Map of Bonne Bay, Newfoundland depicting sampling locations within Bonne Bay. *Note: Black lines indicate location of lobster traps.

2.3.2 Non-invasive sampling techniques

Immediately following capture, fecundity estimates were completed using the first non-invasive sampling technique, the **measurement technique;** the length (A1) and width (A2) of

the entire egg mass (Fig. 2a), was measured using a calliper (0.1mm). The height at each egg segment (A3, A4, A5, A6, and A7; Fig. 2b) was measured using a narrow ruler/depth gauge (~1 cm wide), which was inserted into the center of the egg mass between each segment until it reached the surface of the abdomen (Fig. 2c).

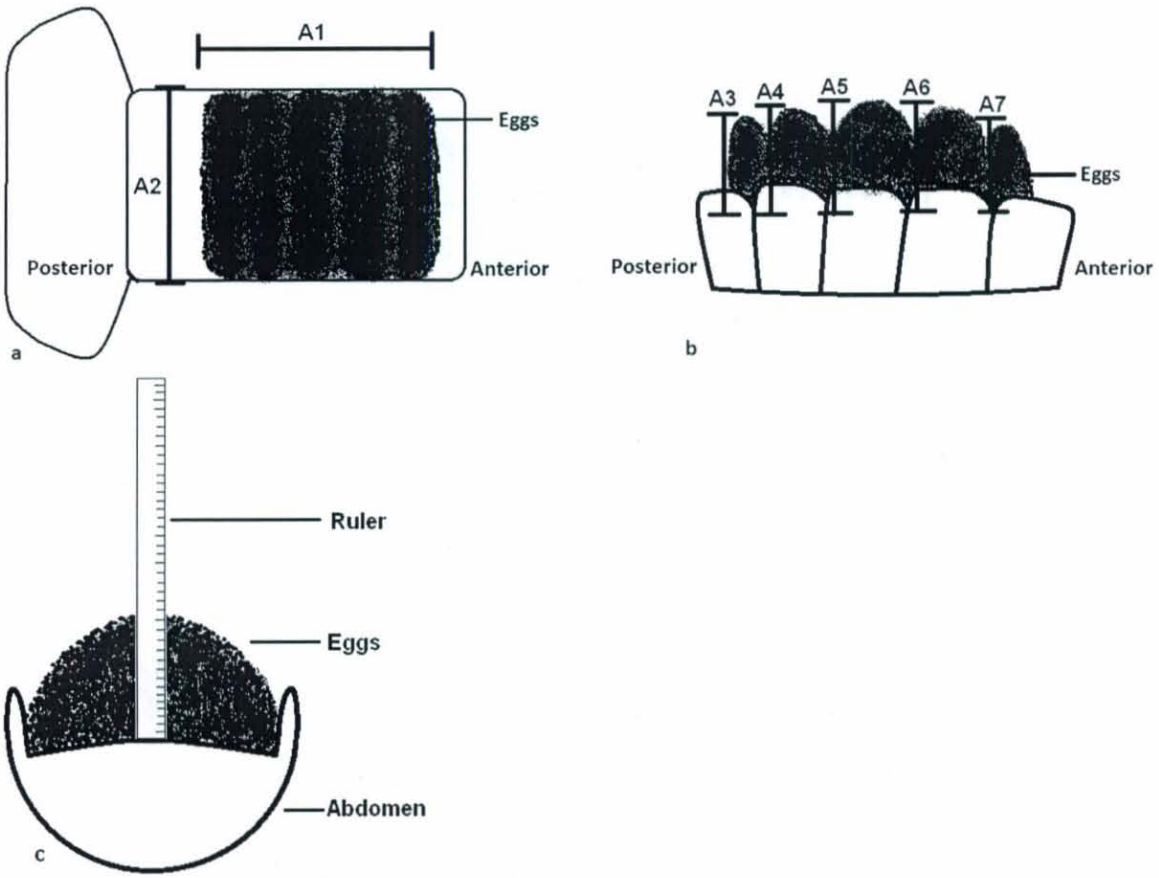

Figure 2. Diagram depicting measurements taken to estimate fecundity using non-invasive sampling technique. (a) Ventral view of an ovigerous lobster abdomen showing length and width measurements of entire egg mass. (b) Side view of an ovigerous lobster abdomen showing egg depth measurements. (c) Cross-section of an ovigerous lobster abdomen showing placement of ruler for measuring egg depth.

For later egg volume calculations, a minimum of 10 eggs were removed randomly from the surface of the egg mass and preserved in 20mL scintillation vials containing a 5% formalin-seawater solution. Once in the lab, the volume of the entire egg mass was calculated by altering the formula for the volume of a cylinder:

$$\text{Volume egg mass} = ((\pi H^2 L)/2)*0.535$$

Where H is the average height of measurements A3, A4, A5, A6, and A7 (Fig. 2b); and L is the length of the entire egg mass, A1 (Fig. 2a). The volume is first halved, because the eggs occur only on the underside of the female abdomen and form half of a cylinder (see Fig. 2c). The volume is then multiplied by 0.535 to account for the packing arrangements of lobster eggs, which have a packing density of 53.5% as a result of empty spaces present between adjacent eggs.

The volume for each egg was calculated using the formula for a sphere:

$$\text{Volume egg} = (4/3\pi r^3)$$

Where r is the radius of the egg, and was calculated by halving the diameter. The diameter was obtained by averaging the longest and shortest axis of 10 eggs, measured using a compound microscope (40X magnification). The influence of preservation on egg diameter was considered minimal.

Following the measurement technique, additional fecundity estimates were made using the second non-invasive technique, the **image analysis technique**; scaled photographs of the egg mass were taken using an Olympus Stylus Tough-6000 waterproof camera. The height of the egg mass was measured at each segment (B1, B2, B3, B4, and B5) using a thin ruler/depth gauge (Fig. 3a). Once in the lab the length (B6) of the egg mass and the diameter of 10 eggs were

measured using the image analysis software ImageJ® (http://rsb.info.nih.gov/ij/; Fig. 3b). The image analysis technique did not require the removal of any eggs.

The volume of the egg mass and the eggs were calculated using the same formulas and methods as the measurement technique, with the exception that egg mass length (L) and egg diameters (D) were measured by analyzing the photograph (Fig. 3b) with the image analysis software.

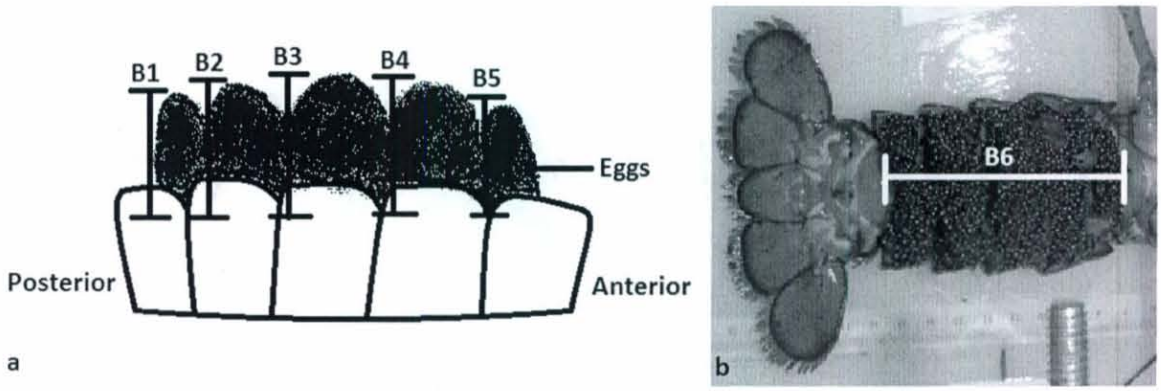

Figure 3. Diagram depicting measurements and photographs taken to estimate fecundity using non-invasive sampling technique. (a) Side view of ovigerous lobster abdomen showing depth measurements. (b) Ventral view of an ovigerous lobster abdomen showing length measurement.

2.3.3 Validation of measurements using traditional invasive technique

Following the non-invasive techniques, the eggs were removed from the females using forceps and fecundity was measured using the commonly practiced **traditional method** (e.g. Ennis, 1981; Campbell and Robinson, 1983; Attard and Hudon, 1987, Estrella and Cadrin, 1995). Eggs were preserved in a 5% formalin-seawater solution for a period of 24 hours and were then washed in freshwater and oven dried at 50°C for 20 hours. Once dried, the eggs were rubbed over a fine screen mesh netting (250μm), to remove any excessive connective tissue, and weighed to the nearest 0.0001g. Fecundity was determined by counting five weighed sub-samples (≥30 eggs/sample) and dividing the weight of an average egg into the weight of the

entire egg mass. These counts were validated by comparing them to four counted samples, and the error ranged from 0.09 % - 0.90 % ($\bar{x}$ = 0.54 %).

2.3.4 Analytical comparisons of non-invasive techniques and the traditional method

For all tests, the statistical program S-Plus (TIBCO Software Inc., Palo Alto, California) was used, and a P-value ≤ 0.05 was considered significant. A paired t-test was used to test the null hypothesis that the mean differences between each non-invasive technique and the traditional method were not significantly different from zero. The percent differences in fecundity estimates from each non-invasive technique and the traditional method were also compared.

2.4 Results and Discussion

2.4.1 Comparison of non-invasive techniques and the traditional method

The fecundity estimates for the measurement technique showed little variation to those from the traditional method, with an average percent difference of ± 3.7% (Table 1). As a result of this similarity, the non-invasive measurement technique was deemed highly reliable. In contrast, the image analysis technique showed little similarity to the traditional method, with an average percent difference of 114.3% and a consistent bias upwards (Table 1). Moreover, the mean difference in fecundity estimates for the image analysis technique and the traditional method were significantly different from zero (Paired t-test, t = 4.07; d.f. = 9; p-value = 0.0028). In contrast, the mean difference in fecundity estimates of the traditional method and the measurement technique were not significantly different from zero. (Paired t-test, t = 1.6285; d.f. = 9; p-value = 0.14).

The overestimation of egg mass length and underestimation of egg diameter most likely accounted for the largest proportion of the differences observed between the results of the image

analysis technique and the measurement technique. The average egg mass length, estimated using the image analysis technique, was 12.6% greater than that obtained using the measurement technique (Table 2). Additionally, the average egg diameter, estimated using the image analysis technique, was 24.33% less than those obtained using the measurement technique (Table 2).

Table 1: Fecundity estimates calculated using two non-invasive techniques and the traditional invasive method, as well as the percent differences between the non-invasive techniques and the traditional method.

Lobster ID	Traditional Method	Measurement Technique	Image Analysis Technique	% Difference Measurement Technique	% Difference Image Analysis Technique
1	11797.56	12128	25898	2.80%	119.52%
2	8320.382	8031	14211	-3.48%	70.80%
3	11181.07	11146	14797	-0.31%	32.34%
4	10378.22	10330	20912	-0.47%	101.50%
5	7542.309	7618	19985	1.00%	164.97%
6	9325.107	9301	17493	-0.26%	87.59%
7	10543.32	10848	15826	2.89%	50.10%
8	13102.44	15334	47483	17.03%	262.40%
9	10602.97	12415	16435	17.09%	55.00%
10	10848.07	10905	32434	0.53%	198.98%
Average				3.68%	114.32%

*% Difference = average percent change between observed values (measurement or image analysis technique) and expected values (traditional method)
= [(observed – expected)/expected]*100.

The percent differences for lobsters 8 and 9 were substantially larger than those for any of the other lobsters (Table 1). This was likely a result of inaccurate measurements of egg height, a highly sensitive parameter in the calculation of egg volume. A change of ±1 mm in the average egg height can alter the fecundity estimates by as much as ±1000 eggs/lobster. As a result, the measurements for egg height must be taken with great precision to ensure accurate fecundity estimates.

Table 2: Measurements taken for estimation of fecundity using the non-invasive sampling techniques.

Lobster ID	Measurement Technique					Image Analysis Technique					% Diff. in Egg Diameter	% Diff. in Egg Mass Length
	Average Egg Length (mm)	Average Egg Width (mm)	Average Egg Diameter (mm)	Egg Mass Length (mm)	Average Egg Mass Depth (mm)	Average Egg Length (mm)	Average Egg Width (mm)	Average Egg Diameter (mm)	Egg Mass Length (mm)	Average Egg Mass Depth (mm)		
1	1.875	1.775	1.825	69	25.8	1.496	1.396	1.446	74.934	25.8	26.18%	8.60%
2	1.731	1.651	1.691	63	19.6	1.409	1.369	1.389	63.072	19.6	21.78%	0.11%
3	1.811	1.791	1.801	67	24.6	1.591	1.371	1.481	88.523	24.6	21.55%	32.12%
4	1.776	1.764	1.770	59	24.6	1.504	1.404	1.454	67.58	24.6	21.78%	14.54%
5	1.817	1.797	1.807	60	21.6	1.333	1.331	1.332	64.561	21.6	35.56%	7.60%
6	1.786	1.754	1.770	54	24.4	1.518	1.498	1.508	64.108	24.4	17.41%	18.72%
7	1.735	1.653	1.694	61	23.2	1.593	1.567	1.580	73.806	23.2	7.20%	20.99%
8	1.858	1.792	1.825	72	28.4	1.314	1.292	1.303	82.998	28.4	40.01%	15.28%
9	1.827	1.795	1.811	64	26.8	1.657	1.627	1.642	64.471	26.8	10.32%	0.74%
10	1.600	1.592	1.596	69	20.0	1.130	1.224	1.127	73.945	20.0	41.54%	7.17%
Average											24.33%	12.59%

The use of a higher caliber camera may have provided more favourable results for the image analysis technique. This would have allowed for more accurate estimations of egg diameter as well as egg length. In addition, there is a magnification factor that needs to be carefully considered when taking calibrated photographs. The objects to be measured in the photograph must be at the same level/height as the device used to calibrate the photograph, in this case a ruler. Deviation from this set height will scale down the measurements, if the object is below the set height, or scale up the measurements if the object is above the set height. This is a problem when photographing lobster eggs still attached to the abdomen of females, since the eggs are attached at many different layers on the abdomen, which becomes indistinguishable in the photographs. As a result, a technique that does not require the removal of any eggs was not achieved.

Automated procedures, using ImageJ software, have been created to measure eggs that are spread out in a monolayer and separated on a flat surface (Kennedy *et al.,* 2007; Klibansky and Juanes, 2008; Faulk and Holt, 2008). This may improve the efficiency of the measurement technique, reducing the time needed to measure egg diameter using a microscope. However, this method should first be tested for accuracy, before being substituted into the measurement technique.

In addition to the image analysis and measurement techniques, various other non-invasive estimates of fecundity were tested. Egg mass volume was computed using the formula for a rectangle and egg volume calculations using the formula for a sphere. The average error associated with this method was 139.82%. Secondly, egg mass volume was computed using the formula for a rectangle and egg volume calculations using the formula for a cube. The average error associated with this method was 25.57%. Finally, egg mass volume was computed using

the formula for a cylinder and then halved, and egg volume using the formula for a sphere. The average error associated with this method was 94.28%.

2.4.2 Egg Packing

These large errors in fecundity estimates may be explained by the packing arrangements of the eggs on a female's abdomen. Spherical objects, such as lobster eggs, may be oriented in one of the following packing arrangements: loose, regular, or irregular, which have densities of 55%, 74%, and 63% respectively (Song *et al.,* 2008; Torquato *et al.*, 2000). These packing arrangements, which were determined using ball bearings, cannot be directly applied to biological specimens, such as lobster eggs, because various untested factors, such as egg aeration and connective tissue, affect the arrangement of eggs on a lobster abdomen. However, final fecundity estimates that used spherical egg volumes largely overestimated egg counts. This suggests that some packing arrangements may be applicable to lobster eggs, since the egg mass volume calculations assumed a density of 100%, which cannot be achieved due to the packing arrangements of spheres. A solution to this problem was presented in the measurement technique, where the final egg mass volume was reduced to a density of 53.5%, reducing the final egg estimates by the appropriate percentage. The reduction in egg mass volume to 53.5% produced the closest estimation of observed egg count, suggesting that lobster eggs display a loose packing arrangement, most likely to allow for aeration of the egg mass.

2.4.3 Implications of non-invasive techniques

In addition to the potential for reducing the effort to estimate fecundity and destructive sampling, the measurement technique presented in this study has some desirable advantages. There have been numerous studies completed on the size-fecundity relationships of *H. americanus* since the first monograph on the species was published by Herrick (1896). A non-

exhaustive literature search revealed that to date these studies have sampled over 7,000 lobsters, removing 138 million eggs, and potentially removing 1.3 million lobsters from the population, assuming a 1% survival rate (Herrick, 1896; Squires, 1970; Squires *et al.*, 1974; Ennis, 1981; Campbell and Robinson, 1983; Estrella and Cadrin 1995). This non-invasive method will prevent the need for future removal of eggs from ovigerous females.

In Atlantic Canada, the Fisheries Resource Conservation Council (FRCC, 1995; 2007) has raised concerns about the sustainability of the fishery for *H. americanus*. High exploitation rates of lobsters of legal size, up to 95% in some areas, consist primarily of immature animals, resulting in extremely low egg production and high risk of recruitment failure (FRCC, 2007), and the removal of eggs from females to create size-fecundity relationships is no longer encouraged. However, many lobster populations would benefit from the development of additional size-fecundity relationships, since there is known geographic variation (Estrella and Cadrin, 1995), and the relationships currently available are not applicable throughout the entire species range. The non-invasive measurement technique presented here would allow for the continued study of the size-fecundity relationships for *H. americanus,* without the detrimental effects of egg removal, as seen in the traditional method.

CHAPTER 3

Latitudinal variation in the size-fecundity relationships of *Homarus americanus* in the Northwest Atlantic

3.1 Abstract

Population parameters for lobsters are known to vary with latitudinal changes in environmental conditions, but a quantitative model, applicable throughout the species range, has not been developed for any parameter. To create such a model, fecundity estimates for the American lobster, *Homarus americanus*, were obtained from 11 locations in the Northwest Atlantic (from the Strait of Belle Isle, Newfoundland to Buzzards Bay, Massachusetts). A two parameter power function, $F=aCL^b$, was used to describe the relationship between carapace length CL and fecundity F. There was a well-defined latitudinal gradient in the allometric exponent b (power law exponent), with the largest values at the southern end of the species range. The relationship between the allometric exponent b and latitude was $b = -0.08597*Lat + 7.0202$ with a standard deviation of 0.0179 on the slope. First approximations for fecundity estimates in data poor location can now be made using the power functions, where b, a power law exponent, and a, a scaling factor, are calculated from latitude.

3.2 Introduction

Current size-fecundity relationships for the American lobster, *H. americanus*, exist from northern Newfoundland to southern New England (Herrick, 1896; Saila *et al.*, 1969; Squires, 1970; Perkins, 1971; Squires *et al.*, 1974; Aiken and Waddy, 1980; Ennis, 1981; Campbell and Robinson, 1983; Attard and Hudon, 1987, Estrella and Cadrin, 1995). These relationships predict fecundity from carapace length and form an empirical foundation for the estimation of life history patterns, population growth, and evaluation of management measures (FRCC, 2007; ASMFC, 2009).

Variability in size-fecundity relationships has been recognized in the literature (Estrella and Cadrin, 1995) and may be explained by differences in experimental methods, geography, and/or sample size (Aiken and Waddy, 1980). The need for additional sampling has been emphasized in the literature to standardize methodologies and increase sample size (Estrella and Cadrin, 1995; Aiken and Waddy, 1980). However, increased fishing effort and economic value has prevented such large scale sampling (Estrella and Cadrin, 1995) and the co-management of the species among fishers and researchers, limits the availability of permits that allow for the removal of eggs from a large number of females. Annual exploitation rates for *H. americanus* are rarely below 80%, with some Lobster Fishing Areas (LFAs) exploiting 95% of the populations (FRCC, 2007; ASMFC, 2009). The increased fishing effort and regulation has presented managers with the difficult task of assessing populations using only a few reliable size-fecundity equations that may not be applicable throughout the entire species range, and emphasizes the need for a general size-fecundity model that is applicable for the entire species range.

Although different investigators have collected data, the timing of studies and methodology used to estimate fecundity, since the 1980's, have been very similar. Validation in counting methods in these studies has produced an average error of less than ±2.0%, and most eggs were removed at similar times near the end of the incubation period, May-June (Ennis, 1981; Campbell and Robinson, 1983; Estrella and Cadrin, 1995).

The published size-fecundity relationships for *H. americanus* are compromised due to small size ranges and the uncorrected bias of log-transformed equations (Estrella and Cadrin, 1995). Size-fecundity relationships are typically represented by a simple two-parameter power function (Ennis, 1981; Campbell and Robinson, 1983; Estrella and Cadrin, 1995). Relationships are rarely examined in their original, arithmetic scale, but are immediately transformed into their logarithmic equivalent and displayed as a bivariate plot with a straight line fitted by the method of least squares (Ennis, 1981; Campbell and Robinson, 1983; Estrella and Cadrin, 1995). Although this standard approach allows investigators to more readily compare results, it introduces bias (Smith, 1984; 1993; Packard, 2009) and may have negative consequences on the predictive power of the relationship (Zar, 1968, Smith 1980; 1984). Bias associated with log transformations include the magnification of outliers (Smith, 1980, 1984), multiplicative error (Smith, 1993), and inaccurate estimates of Y at large values of X (Packard and Boardman, 2008a). Advances in computer based graphics and statistical software eliminates the need to linearize data sets and logarithmic transformations are no longer needed to estimate power law parameters (Packard, 2009).

The objectives of this research were: (1) to quantify geographic variation at three coastal Newfoundland regions; (2) to re-estimate size-fecundity relationships free of bias due to log

transformation; and (3) develop a model to predict size-fecundity parameters *a* and *b* from latitude (°N), which can be easily obtained for any location.

3.3 Materials and Methods

3.3.1 Study area and data collection

Between 3 and 19 June, 2009 a total of 38 ovigerous (egg-bearing) females were sampled from commercial lobster traps in three regions along the west coast of Newfoundland (Fig 4): Barr'd Harbour (n = 12), Lark Harbour (n = 11), and Port aux Basques (n = 14). Lobsters were chosen for fecundity estimates, if the carapace length was either greater than 110 mm or less than 82.5 mm. Intermediate sized lobsters were not selected for fecundity estimates because significant data are available for Newfoundland lobsters found within the size range 82.5 mm to 110 mm carapace length (Ennis, 1981). In order to minimize the number of eggs being removed from the population only lobsters outside this size range were sampled. Additionally, size-fecundity relationships are largely influenced by the larger and smaller values of X and Y and therefore the absence of intermediate sized lobster will have minimal affects on the relationship.

Fecundity measured in this study refers to the total number of eggs the female is carrying externally at the time of sampling. Eggs were removed from the females only if they appeared undamaged from sampling in lobster traps and handling to increase the sample size range. For every ovigerous lobster sampled the following attributes were measured: carapace length (mm), second segment abdomen width (mm), abdomen length (mm), and the presence/absence of a v-notch. Eggs were immediately removed from females upon capture with no holding period to minimize egg loss due to handling. Before releasing the female any eggs remaining attached to the abdomen that could not be removed, were counted to be included in the final fecundity estimate.

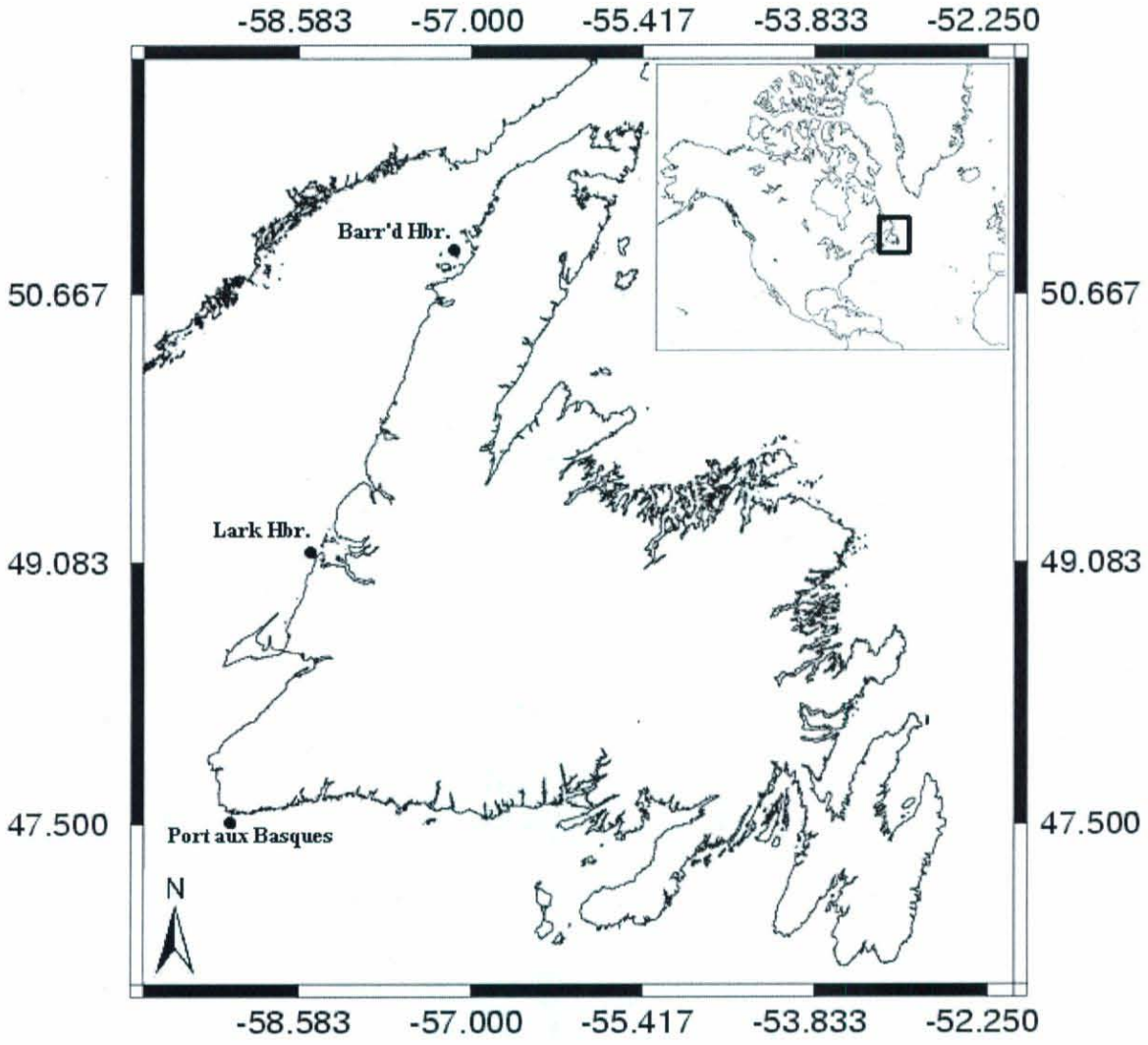

Figure 4. Map depicting the three sampling locations on the west coast of Newfoundland

Eggs were then preserved in 5 % formalin-seawater solution, for a maximum of four weeks, until all samples were collected. After preservation eggs were removed from formalin, rinsed in freshwater, and spread thinly over shallow glass Petri dishes to dry at 50°C for 20 hours (Attard and Hudon, 1987). The dried eggs were rubbed over a fine screen mesh netting (250μm) to remove any excessive connective tissue and weighed to the nearest 0.0001g. Fecundity was

determined by counting five weighed sub-samples (≥30 eggs/sample) and dividing the weight of an average egg into the weight of the entire egg mass. These counts were validated by comparing them to four counted samples, and the error ranged from 0.09 % to 0.90 % ($\bar{x}$ = 0.54 %).

3.3.2 Bias in fecundity estimations

Bias in fecundity estimates could arise from the methodologies used to create size-fecundity equations. Whether the transformation of the raw data (fecundity and carapace length) to their logarithmic equivalents affected the accuracy of fecundity estimates was assessed.

The size-fecundity parameters *a* and *b* were estimated, for all 12 locations, using two different methods. The first used **nonlinear regression:**

Eq. 1: $F = a*CL^b$

where *F* is fecundity, *a* is a scaling factor, *CL* is the carapace length, and *b* is a power law exponent. The second method involved transforming fecundity and carapace length into the logarithmic equivalent, and **log linear regression** used to formulate the appropriate equation, in the following form:

Eq. 2: $\ln(F) = b*\ln(CL) + \ln(a)$

where *F* is fecundity, *b* is the power law exponent from eq. 1, *CL* is the carapace length, and *a* is the scaling factor from eq. 1. This equation was then back transformed to obtain estimates of parameters *a* and *b*.

The ability of these two equations to accurately estimate fecundity was tested by comparing predicted values of fecundity to observed values, from 11 locations throughout the Northwest Atlantic. The bias associated with each method was recorded, and paired t-tests were used to test the null hypothesis that the mean differences between the observed values of fecundity and those estimated were not significantly different from zero.

3.3.3 General model and data analysis

For all tests and analyses, the statistical programs S-Plus® (TIBCO Software Inc., Palo Alto, California, 2010) and R® (R Development Core Team, 2010) were used, and a P-value $\leq$ 0.05 was considered significant. Raw fecundity data for five sites in Newfoundland waters (Ennis, 1981), three sites off Nova Scotia (Campbell and Robinson, 1983) and five sites in Massachusetts waters (Estrella and Cadrin, 1995; Herrick, 1896) were acquired from the authors. The data were re-evaluated and fitted to a two parameter power function using nonlinear least squares regression in R® (R Development Core Team, 2010) obtaining new estimates for parameters *a* and *b*. A paired t-test was used to test the null hypothesis that the mean differences between the slopes (parameter *b*) calculated using nonlinear least squares regression and log linear regression were not significantly different from zero.

Analysis of covariance was then used to test for regional differences in size-fecundity relationships. Data sets that had narrow size ranges and were located in the same geographic region were tested for differences in slopes. If the comparison between two locations exhibited homogeneity among size-fecundity relationships (p-value > 0.05), the data were combined to increase the size range and sample size.

Latitude for each location was obtained from the primary literature if provided, or a map. If locations were combined the average latitude was used. Latitude (°N) was then converted into decimal degrees to aid in graphical analysis, using the following formula:

Eq. 3: $Lat = dd° + \{[mm' + (ss.ss''/60)]/60\}$

where *Lat* is Latitude, *dd* is degrees, *mm* is minutes, and *ss.ss* is seconds with two decimal places.

Once the data sets were combined, two general models to estimate size-fecundity relationships were formulated. The first model, **Latitude Model # 1** was developed using the following equations:

The relation of parameter *b* to latitude was estimated using the following equation:

$$\textbf{Eq. 4 :}\ b = m_1 * Lat + g_1$$

where *b* is the power law exponent from eq. 1, m_1 is the slope, *Lat* is Latitude, and g_1 is the intercept.

The relation of parameter *a* to parameter *b* was estimated using a nonlinear, 3-parameter, exponential decay equation, which showed a strong relationship between parameter *a* and *b*:

$$\textbf{Eq. 5 :}\ a = c + de^{-f * b}$$

where *a* is the scaling factor from eq. 1, *c* is the intercept, *d* is a scaling factor, *f* is an exponential decay rate, and *b* is the power law exponent from eq. 1.

In addition to analyses with the Latitude Model # 1, data were re-analysed using a **Latitude Model # 2**, where parameter *b* was calculated using the same equation as in Latitude Model # 1, but parameter *a* was calculated in two steps. First the average fecundity at 85 mm carapace length was calculated from latitude using the following formula:

$$\textbf{Eq. 6:}\ F(avg) = m_2 * Lat + g_2$$

where *F(avg)* is the average fecundity at 85 mm carapace length, m_2 is the slope, *Lat* is the latitude, and g_2 is the intercept.

Eighty-five millimetres carapace length was used because it was the size class available at most locations and provided the largest sample size to develop equation 6.

Secondly, the average fecundity and parameter *b* were then substituted into the following equation to solve for parameter *a*:

Eq. 7 : $a = F(avg)/(CL^{b})$

where a is the scaling factor from eq. 1, $F(avg)$ is the average fecundity from eq. 6, CL is 85 mm carapace length, and b is the power law exponent from eq. 1.

The efficacy of Latitude Model # 1 and # 2 were tested by comparing the fecundity values predicted by the models to those of the observed values. The bias associated with each model was recorded, and paired t-tests were used to test the null hypothesis that the mean differences between the observed values of fecundity and those estimated were not significantly different from zero.

Comparisons of fecundity estimates, made using the published fecundity equation and the Latitude Model # 2 equation to that of the observed fecundity, were graphed for all 12 locations (Appendix 1). Furthermore, the overestimation of fecundity for larger lobsters using the published equation for Buzzards Bay was illustrated in Appendix 2.

3.4 Results

3.4.1 Newfoundland fecundity equations

Analysis of size-fecundity relationships with nonlinear regression showed Port aux Basques to have a steeper slope then Lark Harbour and Barr'd Harbour, which displayed similar slopes (Fig. 5; Table 3). Extra-sum-of-squares *F*-tests (Motulsky and Christopoulos, 2004) were carried out to evaluate differences in the slopes of the size-fecundity relationships from the west coast of Newfoundland. When testing only the differences in slopes for the three regression lines, they were found to be significantly different. ($F_{2,27} = 4.1437$, P-value = 0.0270; Table 4). The slope for Port aux Basques was significantly different from that of both Barr'd Harbour ($F_{1,17} = 5.2572$, P-value = 0.0349; Table 5) and Lark Harbour ($F_{1,17} = 4.9178$, P-value = 0.0405; Table 6). Slopes for Barr'd Harbour and Lark Harbour were not significantly different ($F_{1,20} = 0.7071$,

P-value = 0.1453; Table 7) and were therefore combined to produce the following equation (Fig. 6):

$$F = 0.049*CL^{2.815}$$

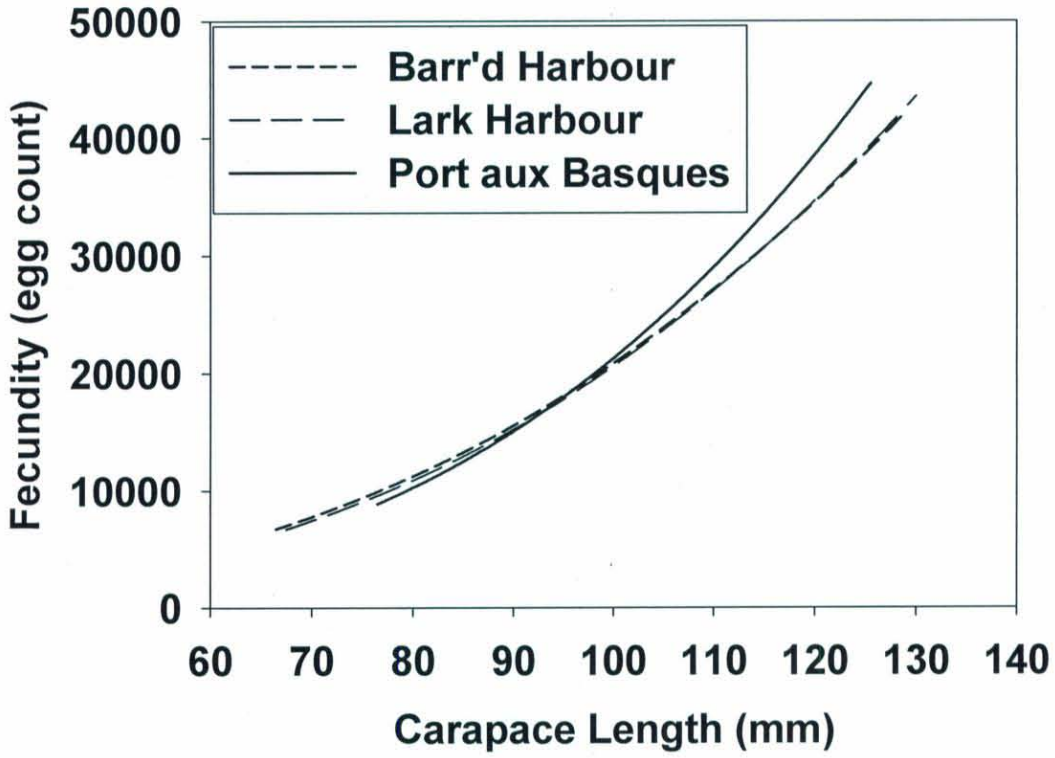

Figure 5. Size-fecundity relationships for *H. americanus* on the west coast of Newfoundland. Barr'd Harbour (n=12): $R^2 = 0.98$, standard error (S.E.) on slope ± 0.1789. Lark Harbour (n=11): $R^2 = 0.98$, S.E. on slope ± 0.1431, Port aux Basques (n=9): $R^2 = 0.95$, S.E. on slope ± 0.4056.

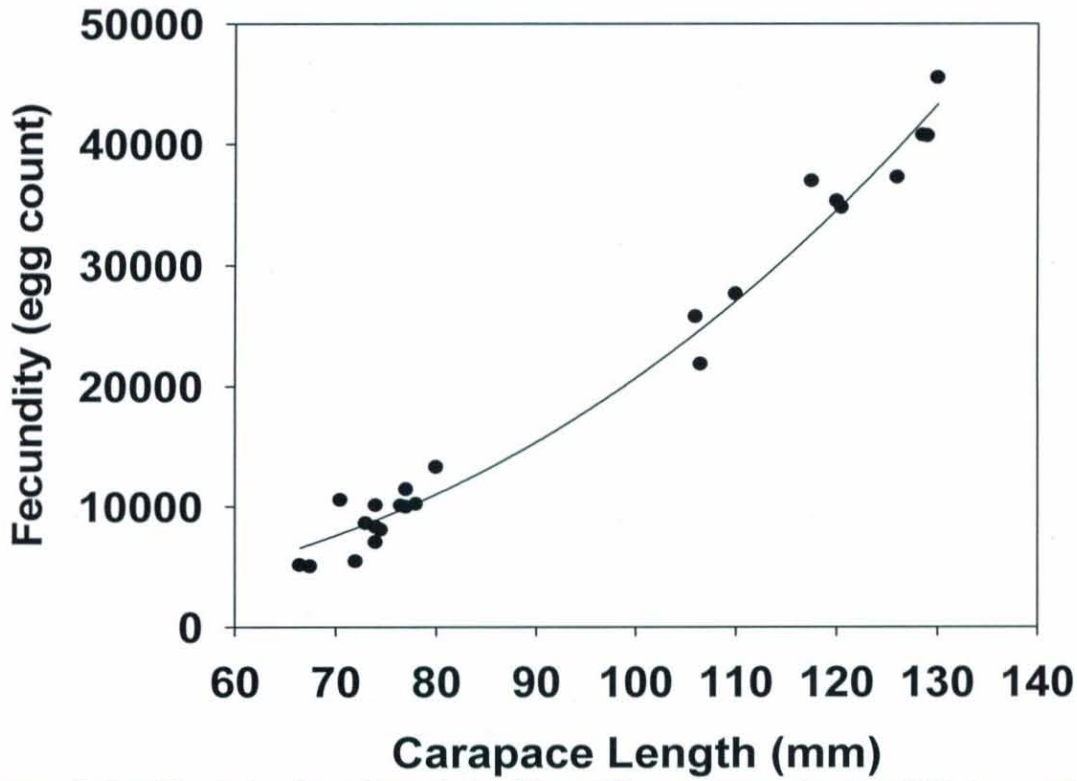

Figure 6. Combined size-fecundity relationships of *H. americanus* for Barr'd Harbour and Lark Harbour on the west coast of Newfoundland. $R^2 = 0.98$, S.E. on slope ± 0.1092.

A second analysis was used to test for differences in both slopes and intercepts for Port aux Basques, Lark Harbour, and Barr'd Harbour and this analysis found no significant difference among location ($F_{4,27} = 2.3608$, P-value = 0.078; Table 8).

Residual versus fit and Quantile-Quantile plots were used to evaluate the residuals for violations of assumptions for computing p-values. If the models violate assumptions of normal and homogenous residuals, the p-values are considered invalid. All models displayed homogenous (Fig. 7) and normally distributed (Fig. 8) residuals.

Table 3. Size-fecundity relationships for *H. americanus* on the west coast of Newfoundland.

Site	Latitude (°N)	n	*a*	*b*	R^2
Barr'd Harbour	50.8497	12	0.0600	2.7703	0.9796
Lark Harbour	48.9743	12	0.0399	2.8564	0.9849
Port aux Basques	47.6606	9	0.0063	3.2652	0.9465

* Five lobsters were removed from Port aux Basques sample, due to egg loss as a result of holding tanks.

Table 4. Summary of ANOVA testing for differences in slopes of the size-fecundity relationships for Barr'd Harbour, Lark Harbour, and Port aux Basques located on the west coast of Newfoundland.

Source	DF	SS	MS	F	P-value
Location	2	62165954	31082977	4.143725	0.026949
Error	27	202532835	7501216		
Total	29	264698789			

Table 5. Summary of ANOVA testing for the differences in slopes for Barr'd Harbour and Port aux Basques.

Source	DF	SS	MS	F	P-value
Location	1	52457280	52457280	5.257179	0.034881
Error	17	169629702	9978217.8		
Total	18	222086982			

Table 6. Summary of ANOVA testing for the differences in slopes for Lark Harbour and Port aux Basques.

Source	DF	SS	MS	F	P-value
Location	1	45075271	45075271	4.917765	0.040496
Error	17	155818686	9165805.1		
Total	18	200893957			

Table 7. Summary of ANOVA testing for the differences in slopes for Barr'd Harbour and Lark Harbour.

Source	DF	SS	MS	F	P-value
Location	1	578389	578389	0.1453	0.7071
Error	20	79617282	3980864		
Total	21	80195670			

Table 8. Summary of ANOVA testing for differences in slopes and intercepts at three locations for the west coast of Newfoundland.

Source	DF	SS	MS	F	P-value
Location	4	70836983	17709246	2.36085	0.07845
Error	27	202532835	7501216		
Total	31	2733698173			

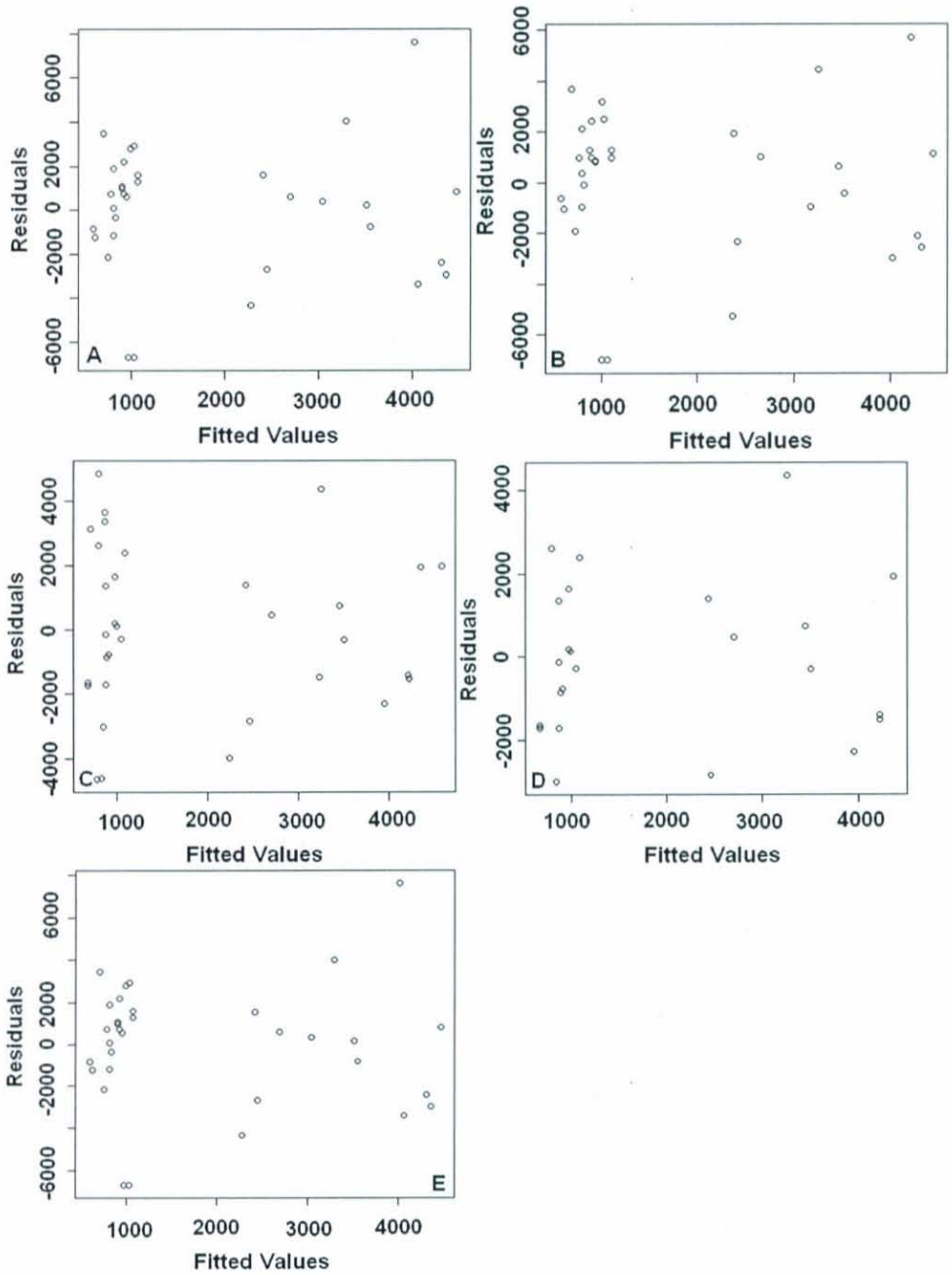

Figure 7. Residuals and fitted values plotted from various models to evaluate the assumption of homogenous residuals: Residuals vs. fits plot testing for differences in slopes for the west coast of Newfoundland (A), Barr'd Harbour and Port aux Basques (B), Lark Harbour and Port aux Basques (C), Barr'd Harbour and Lark Harbour (D). Residuals vs. fits plot testing for differences in slopes and intercepts for the west coast of Newfoundland (E).

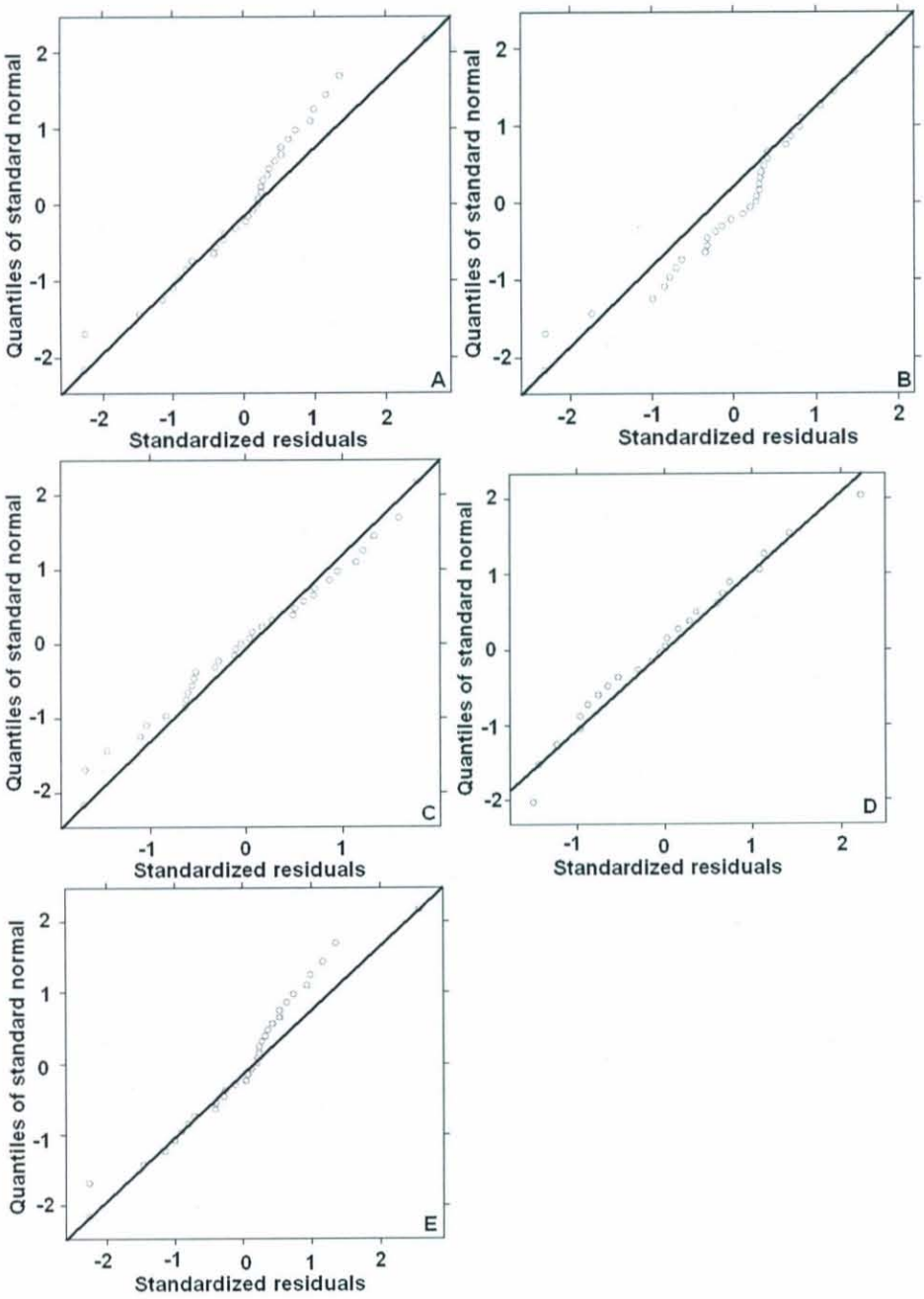

Figure 8. Quantile-quantile plots for various models to evaluate normality of residuals: Quantile-quantile plot testing for differences in slopes for the west coast of Newfoundland (A), Barr'd Harbour and Port aux Basques (B), Lark Harbour and Port aux Basques (C), Barr'd Harbour and Lark Harbour (D). Quantile-quantile plot testing for differences in slopes and intercepts for the west coast of Newfoundland (E).

3.4.2 General Model

To develop a general model, data sets with large size ranges were needed to ensure estimates of parameters *a* and *b* were not skewed. As a result, locations with similar latitudes were tested for homogeneity of slopes. Ship Harbour (SH) and Boswarlos (BOS), and Ship Harbour and Arnolds Cove (AC) showed significant differences among slopes (Table 9), and were not included in the analysis because they all displayed narrow size ranges. The Northumberland Strait (NUS) and the Bay of Fundy (BOF), Buzzards Bay (BB) and Outer Cape Cod (OCC), and Barr'd Harbour (BH) and Lark Harbour (LH) all showed homogeneity among slopes (Table 9). These six data sets were then combined into three and the latitudes averaged, increasing their size range for use in the analysis of geographic variation (Table 10; Fig. 9). Paradise (PAR) and the Southern Gulf of Maine (SGM) were also included in the analysis because they displayed large size ranges (Table 10). Temporal variations in size-fecundity relationships were tested and found to be negligible.

Table 9. Summary of ANCOVA testing for homogeneity among slopes of American lobster size-fecundity relationships.

		Slope	
Location	**DF**	**F-value**	**P-value**
BB vs. OCC	284	2.079	0.1505
SH vs. BOS	142	4.4833	0.03601
SH vs. AC	110	5.7555	0.01817
BH vs. LH	23	1.453	0.7071
NUS vs. BOF	123	2.4322	0.1215

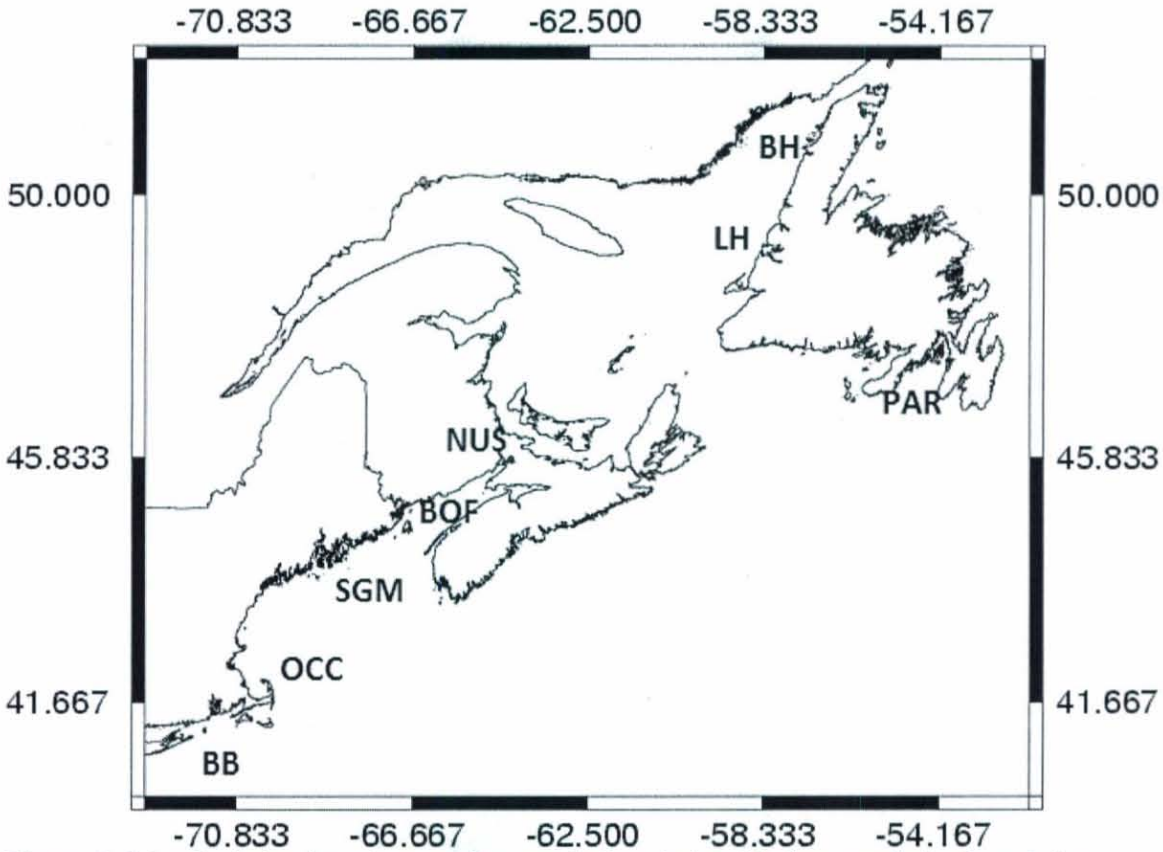

Figure 9. Map depicting locations used to graph the relationship between latitude and size-fecundity parameter *b*

Table 10. Sites used to graph the relationships between latitude and the size-fecundity parameter *b*.

Site	Symbol	Size range	Latitude (°N)	*a*	*b*
Buzzards Bay and Outer Cape Cod	BB+OCC	71-143	41.650	0.003	3.368
Southern Gulf of Maine	SGM	72-137	42.200	0.001	3.496
Northumberland Strait and Bay of Fundy	NUS+BOF	65-163	44.962	0.007	3.188
Paradise	PAR	75-139	47.446	0.053	2.790
Barr'd Harbour and Lark Harbour	BH+LH	67-130	49.912	0.049	2.815

3.4.3 Latitude Model # 1

The relation between parameter *b* and Latitude used in the development of Latitude Model # 1 and 2 was found to be (Fig. 10):

Eq. 4: $b = -0.0859708305 * Lat + 7.0202045476$

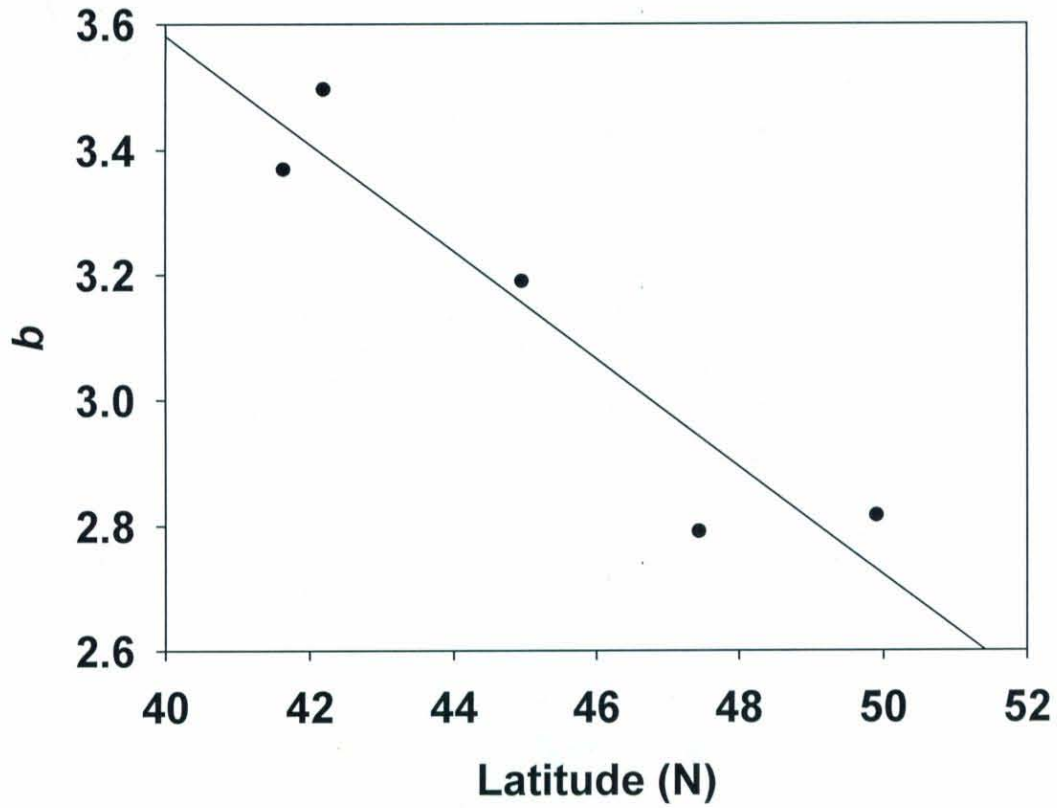

Figure 10. Relationship between parameters *b* (power law exponent) and Latitude. $R^2 = 0.8845$, S.E. on slope ± 0.0179 1/°N.
*Only locations with large size ranges were included.

The relation between parameter *a* and *b* used to solve for parameter *a* in Latitude Model # 1 was (Fig. 11):

Eq. 5: $a = -0.0008 + 8725.1e^{-4.3033 * b}$

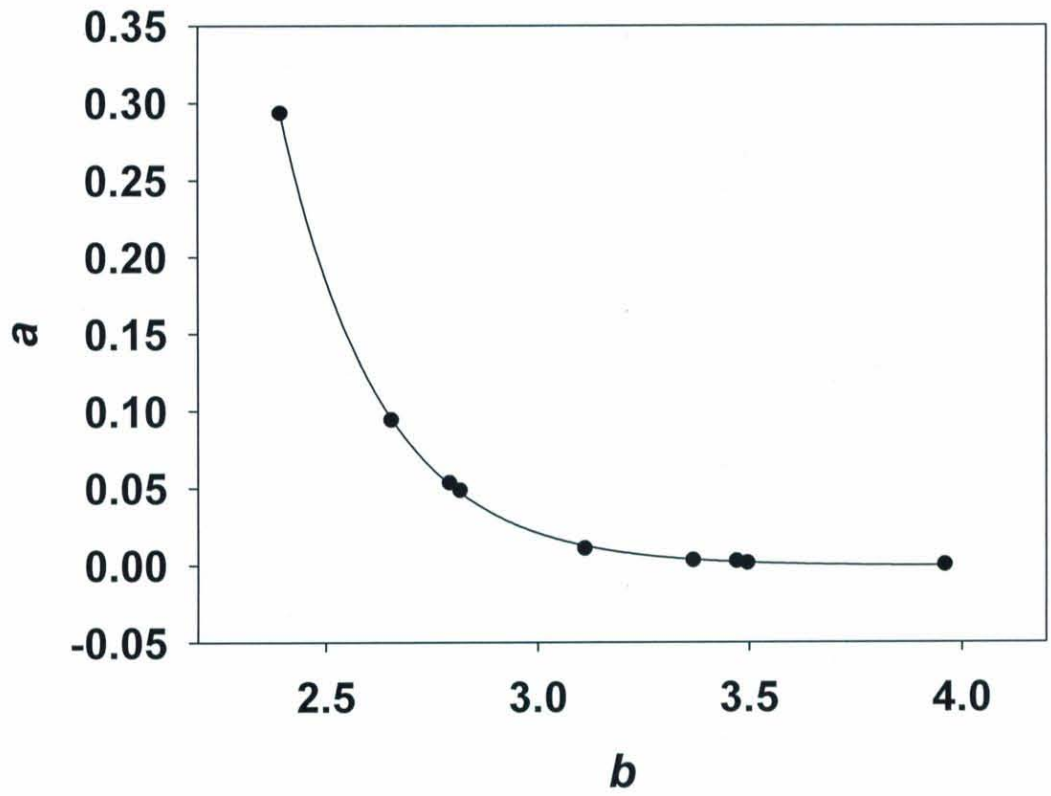

Figure 11. Relationship between parameter *a* (scaling factor) and *b*. $R^2 = 0.99$.

3.4.4 Latitude Model # 2

The relation between the average fecundity and Latitude used to develop Latitude Model # 2 was (Fig. 12):

Eq. 6: $F(avg) = 490.5819 * Lat - 12221.6192$

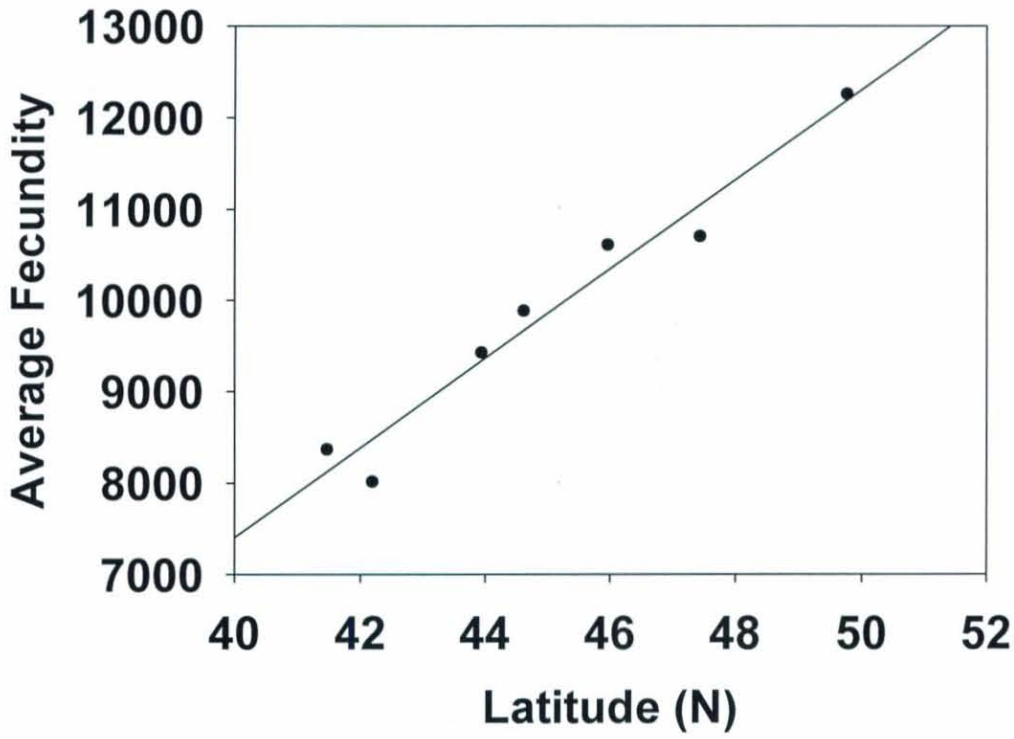

Figure 12. Relationship between the Average Fecundity at 85 mm carapace length and Latitude. $R^2 = 0.96$, S.E. on slope of ± 45.502 eggs/°N.
*The average fecundity at 85 mm CL was only available for 7 locations.

3.4.5 Sources of bias

Re-analysis of the experimental fecundity data obtained from Herrick (1896), Ennis (1981), Campbell and Robinson (1983), and Estrella and Cadrin (1995) with nonlinear regression

revealed changes in the estimates of parameters *a* and *b* (Table 11). Parameter *a*'s calculated using nonlinear regression differed from those calculated using log linear regression, with an average percent difference of 221.63%. Alternately, parameter *b*'s, calculated using nonlinear regression were similar to those calculated using log linear regression, with an average percent difference of 3.4%. However, the mean differences between the slopes calculated using non linear regression and log linear regression were not significantly different from zero (Paired t-test, t = -0.8874; d.f. = 11; p-value = 0.3939) indicating that the value of the slope is not dependent upon the type of regression used, non linear or linear.

Table 11. Comparisons of published estimates of fecundity parameters *a* and *b* to those estimated using nonlinear regression.

	Log transformed linear Equation		**Nonlinear Equation**	
Area	***a***	***b***	***a***	***b***
Newfoundland				
-Arnold's Cove (AC)	0.0045324	3.347062	0.002641	3.47012
-Paradise (PAR)	0.0126958	3.098418	0.05339	2.78993
-Ship Harbour (SH)	0.4878664	2.318816	1.36201	2.10847
-Boswarlos (BOS)	0.0211542	2.938735	0.001862	3.49668
-North-western coast (NWC)	0.3982538	2.316141	0.293255	2.39308
Canadian Maritimes				
-Northumberland Strait (NUS)	0.0000482	4.320195	0.000542	3.77922
-Eastern Nova Scotia (ENS)	0.0000586	4.272524	0.000251	3.9592
-Bay of Fundy (BOF)	0.0031829	3.353501	0.007236	3.19005
New England				
-Southern Gulf of Maine (SGM)	0.0009198	3.580220	0.001443	3.49574
-Outer Cape Cod (OCC)	0.0127547	3.062789	0.006338	3.21765
-Buzzard's Bay (BB)	0.0000764	4.175060	0.000523	3.75921
-Southern Massachusetts (SM)	0.0005640	3.722690	0.0019619	3.47028

*Estimates for published equations are based on log-log transformations.

3.4.6 Validation of fecundity estimates obtained using various models

Fecundity estimates obtained using nonlinear regression, Latitude Model # 2, and log linear regression were similar to the observed values, having percent bias of -3.94%, -4.39, and -5.2 respectively (Table 12). In contrast, Latitude Model # 1, differed from the observed values of fecundity and the estimates, having an average percent bias of -22.5% (Table 12). In addition, the mean differences in the observed values of fecundity and the estimated values obtained using log linear regression (t-test, t = -2.3537: d.f. = 10; p-value = 0.0404) and Latitude Model # 1 (t-test, t = -2.5487; d.f. = 10; p-value = 0.0289) were significantly different from zero. In contrast, the mean differences in the observed values of fecundity and the estimated values obtained using nonlinear regression (t-test, t = -1.9325; d.f. = 10; p-value = 0.0821) and the Latitude Model # 2 (t-test, t = 1.1316; d.f. = 10; p-value = 0.2842) were not significantly different from zero.

Table 12. Bias associated with differing methods of fecundity estimations.

Loc.	Non Linear regression		Log linear regression		Latitude Model # 1		Latitude Model # 2	
	Bias[1]	% Bias[2]	Bias	% Bias	Bias	% Bias	Bias	% Bias
SGM	-627	-5.44	-1344	-8.97	-21422	-138.92	-1115	9.66
BB	-606	-4.82	-1130	-7.80	-12995	124.42	1070	-9.73
OCC	990	1.59	1230	1.17	-27269	-95.76	4550	-15.68
AC	-341	-1.39	-291	-1.51	1494	8.73	-2306	-14.45
BOS	264	1.35	841	3.80	-624	-9.18	-613	8.88
NWC	-45	-9.05	-2	-9.20	454	-3.66	-557	-10.74
PAR	-96	2.53	-1245	-4.25	819	1.69	2645	-9.15
SH	-842	-4.02	-1203	-3.53	-3090	-4.87	-397	-2.99
BOF	-1434	-6.21	-1850	-5.92	-20924	-56.69	1471	-2.21
ENS	-1289	-10.9	-1562	-11.27	-4705	-39.10	1866	-7.37
NUS	-386	-7.01	-1452	-9.72	-1152	-34.59	658	5.47
Avg.	-401	-3.94	-728	-5.20	-8128	-22.50	661	-4.39

[1]Bias = average difference in egg count from observed values and estimated values
= observed – estimate.

[2]% Bias = average percent change between observed values and expected values
= [(observed – expected)/expected]*100.

Note: Herrick's (1896) data was not included because total length measurements were used. See appendix 1 for further details on bias in latitude model # 2

3.5 Discussion

3.5.1 Geographic variation in size-fecundity relationships

An important result of this research is the latitudinal gradient in the size-fecundity parameter *b* (Fig. 10) and the average fecundity at a fixed size class (Fig. 12), which shows conclusively, regional differences in size-fecundity relationships of *H. americanus.* Furthermore, these results suggest differences in the reproductive potential of female lobsters from Newfoundland to Massachusetts. Temperature is the major factor affecting size at maturity, oocyte maturation, spawning incidence, timing and synchronization, success of egg attachment and incubation, and time of hatching (Templeman, 1936, Aiken and Waddy, 1989; Waddy and Aiken, 1991), and is likely the cause for much of the observed geographic variation in the size-fecundity relationships.

The major impediments to evaluating geographic variation in size-fecundity relationships to date has been the confounding effects of obtaining eggs with comparable developmental stages (Ennis, 1981), similar size ranges, and the ability to obtain relationships with high R^2 values (Waddy and Aiken, 1991). To obtain comparisons with similar egg developmental stages, data were restricted to samples obtained during the spring (April-June), with the exception of the Bay of Fundy. Additionally, large size ranges were used to eliminate the confounding effects that small size ranges have on estimates of parameters *a* and *b*. Finally, results obtained had high R^2 values, ranging from 0.88 to 0.99.

Campbell and Robinson (1983) evaluated the differences in the size-fecundity relationships of *H. americanus* in three maritime regions, Eastern Nova Scotia, The Bay of Fundy, and the Northumberland Strait. Their analysis revealed no significant differences in the relationships and the data were condensed into a single equation used in Maritime stock

assessments (*e.g.* Lanteigne *et al.*, 1998). However, the size ranges for each location were narrow spanning only 40 mm carapace length and it has been suggested that broad size ranges are needed to accurately evaluate such differences (Estrella and Cadrin, 1995). When formulating new size-fecundity equations for the three maritime regions using the Latitude Model # 2 the predictive power of the equations increased substantially (Table 12) over those originally presented by Campbell and Robinson (1983), because the Latitude Model # 2 is not affected by small size ranges at any one location. Changes in parameters *a* and *b* will alter the size-fecundity relationships and have notable impacts on fecundity estimates.

Research on regional differences in abdomen area, carapace length, and chelae length has been carried out in Nova Scotia coastal regions (MacCormack and DeMont, 2003). Results of this study showed that the scaling factor of abdomen area with carapace length varied with region. During spawning, female *H. americanus* release their eggs onto the ventral surface of their abdomen, and it has been shown that a larger abdomen area allows for higher egg masses (Templemen, 1935, Atema and Voigt, 1995). This is in accordance with our results, which show distinct differences in the size-fecundity equations with region. The differences observed are thought to be the result of varying temperatures. The northern and southern limits of the *H. americanus* experience extreme differences in the range and duration of cold and warm water temperatures and these differences are known to effect egg production (Waddy and Aiken, 1991).

The observed trend in fecundity estimates throughout the species range may be explained by differences in growth rates. Newfoundland lobsters are known to grow at slow rates when compared to lobsters found in more southern locations such as Southern Gulf of Maine (Ennis, 1980). In this study, lobsters occurring in colder waters tended to have higher egg counts at

smaller sizes up to 110 mm CL. This could be explained by a slower growth rate which would require the lobsters to produce more eggs at smaller sizes, since they would require a longer time period to reach larger sizes. Further research and variations in egg size with latitude could help explain the observed trend.

The observed latitudinal trend in size-fecundity relationships may also be due to differences in size at first maturity. It is a well accepted fact that lobsters reproduce at smaller sizes in warm waters (Aiken and Waddy 1976). The results suggest that lobsters of smaller size from southern location would have fewer eggs; however, this may not be the case. The relationships may be influenced by the earlier maturation of lobster in the southern locations when compared to northern location giving the impression of fewer eggs at smaller size. Further research on comparisons of fecundity estimates of lobsters at sizes just above their ages at maturity is needed and would aid in the explanation of the observed trends.

3.5.2 Biases in Analysis

The power function has long been the favoured model to relate morphological, physiological, or ecological variables of interest to some measure of body size or weight (Packard and Boardman, 2008a; Packard, 2009). However, investigators often prefer to work with logarithmically transformed data and therefore express the power function in its logarithmic equivalent, using log linear regression (Peters, 1983). Analysis of size-fecundity relationships for *H. americanus* has almost always been carried out on the log transformed data (e.g. Campbell and Robinson 1983). Similar to the results presented by Estrella and Cadrin (1995), the results from this study show that size-fecundity equations formed by carrying out nonlinear regression on the raw data are better able to predict the observed values of fecundity (Table 12). Estrella and Cadrin (1995) suggested the use of a correction factor (Sprugel, 1983) for data analysed

using log-transformed data. However, given the better fit of nonlinear regression and the numerous biases associated with log-transformed linear regression (Packard, 2008), it is recommended that future analysis of size-fecundity relationships be made using nonlinear least squares regression.

Results from this study show that a narrow size range affects the estimates of size-fecundity parameters *a* and *b* more readily than a small sample size. Both Lark Harbour and Barr'd Harbour had small sample sizes (n=12), but had a wide range of carapace lengths, spanning over 60 mm from the smallest size to the largest, and had high R^2 values around 0.98. This is largely due to the influence that small and large values of the X and Y have on the estimated parameters. In cases of limited size range of samples, estimates beyond the range are often unreasonable resulting in large overestimations of egg counts (Appendix 2). Additionally, log transformation of data amplifies this overestimation, since small values of the response variable will have greater influence than large values on parameters obtained by fitting a linear equation to the logged data (Packard and Boardman, 2008b). Further research on the effects that sample size has on size-fecundity parameters *a* and *b* is needed.

3.5.3 Latitude models

It is likely that a large proportion of the difference observed between the ability of the two latitude models to predict observed fecundity is because Latitude Model # 2 was not influenced by size range and sample size when predicting parameter *a*. Latitude Model # 2 used a fixed carapace length of 85 mm, and therefore was not influenced by differences in size range. Although parameter *b* was calculated in the same way for both models, calculation of parameter *a* in Latitude Model # 1, was determined from an equation that did not correct for the distorting

effects of small size ranges on size-fecundity parameters *a* and *b*, resulting in large bias in the estimates of fecundity (Table 12).

The fishery for *H. americanus* in the United States and Canada has a total of 48 different management zones (DFO, 2009). A total of thirteen size-fecundity relationships have been developed (Factor, 1995) and are available for use in the management of these 48 different zones. As a result of geographic variation, potential differences in the size-fecundity relationships of lobster in these zones may exist. As a result, research using equations from different regions may produce inaccurate estimates of fecundity. The development of the Latitude Model # 2, presented in this study, will allow data poor locations to formulate size-fecundity equations from latitudes. Stock assessments and yield and egg per recruit models can now use customized size-fecundity relationships, which can be developed for any site from latitude, as first and best approximations of fecundity.

CHAPTER 4

4.1 Conclusion

The research presented here focused on the size-fecundity relationships of *H. americanus* in an effort to improve the co-management of the species among fishers and scientists. Objectives included the development of a non-invasive sampling technique that can accurately estimate fecundity for *H. americanus*, without requiring the removal of eggs, and the development of a general model that can predict size-fecundity relationships for *H. americanus* throughout the entire species range. Results include a minimally-invasive method for estimating fecundity that requires the removal of only a few eggs, as well as a method for developing size-fecundity equations using latitude.

The non-invasive technique requires the measurement of various dimensions of egg mass, as well as the average diameter of ten eggs. This new method now allows for the accurate estimation of fecundity, without requiring the removal of entire egg masses from females. The co-management of the species among fishers and scientists limits the availability of permits that allow for the removal of eggs from a large number of females, and makes this technique appealing for future work on the size-fecundity relationships for the American lobster.

The Latitude Model # 2 allows for the estimation of size-fecundity parameters *a* and *b* by simply substituting latitude into two simple equations. Size-fecundity equations used in stock assessments and yield and egg per recruit models can now be generated for any region, from as far south as Massachusetts and as far north as Newfoundland, to make initial approximations of fecundity.

High exploitation rates and uncertainty in the stability of the fishery for *H. americanus*, prevents the future large scale sampling needed to properly represent the size-fecundity

relationships of the species. Utilization of the currently available size-fecundity data has allowed for the development of the Latitude Model # 2, which estimates size-fecundity equations from latitude, eliminating the need for the development of additional size-fecundity relationships. However, if fecundity estimates, beyond first approximations from latitude, are needed, the non-invasive measurement technique presented in this study can be used. For example, fecundity estimates may wish to be made for lobsters that occur in unique environments, are of a different species, or part of an offshore population. The non-invasive measurement technique provides an accurate estimate of fecundity without the detrimental effects of egg removal from ovigerous females.

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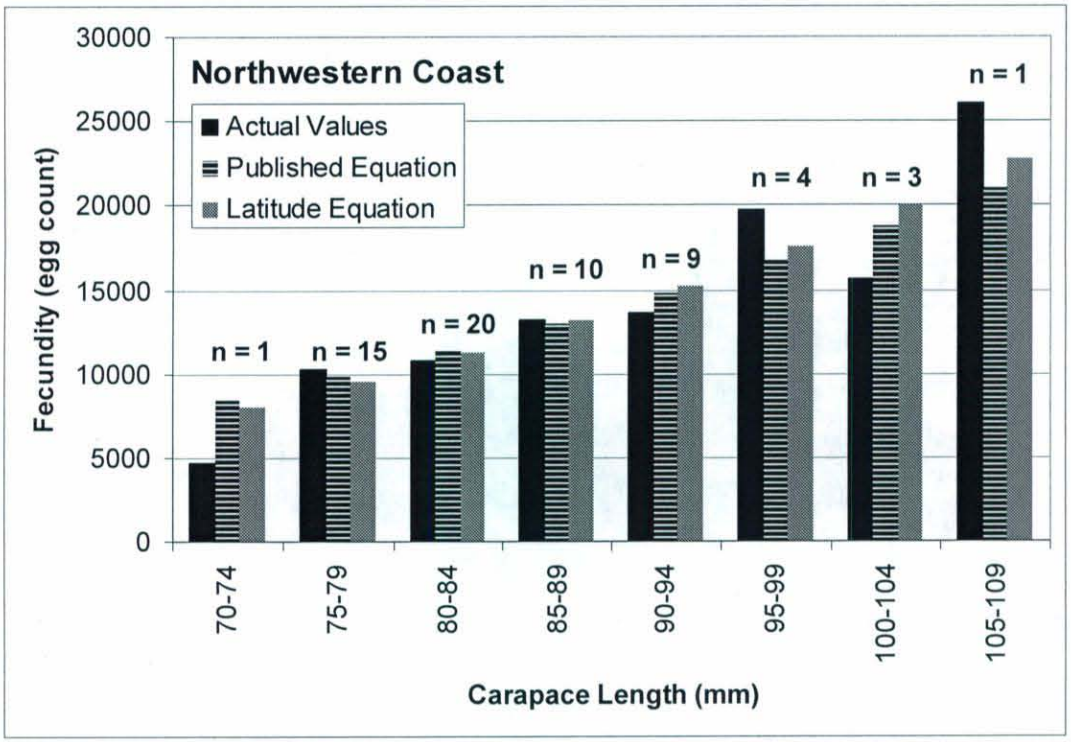
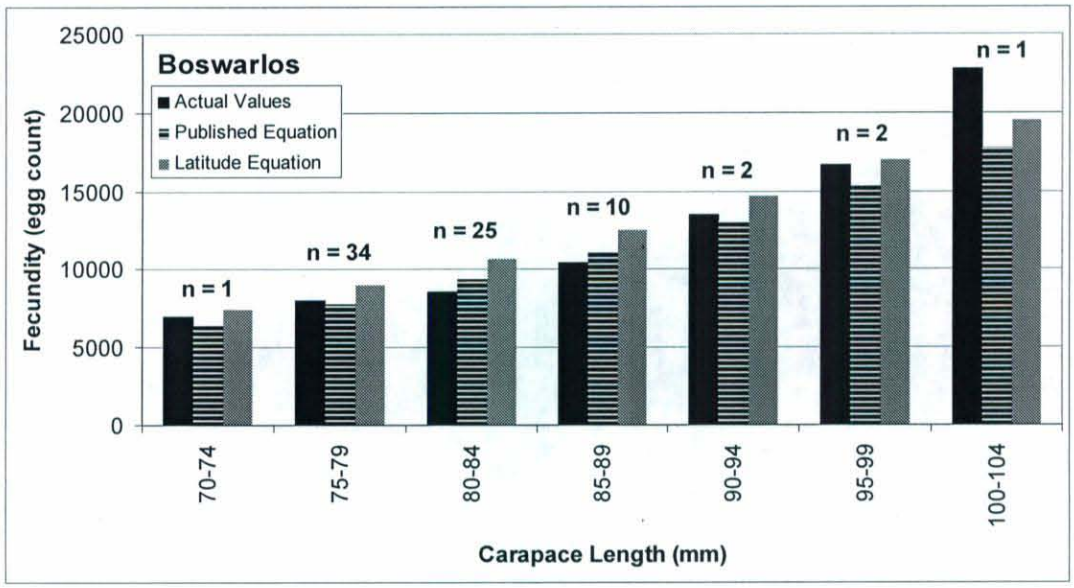
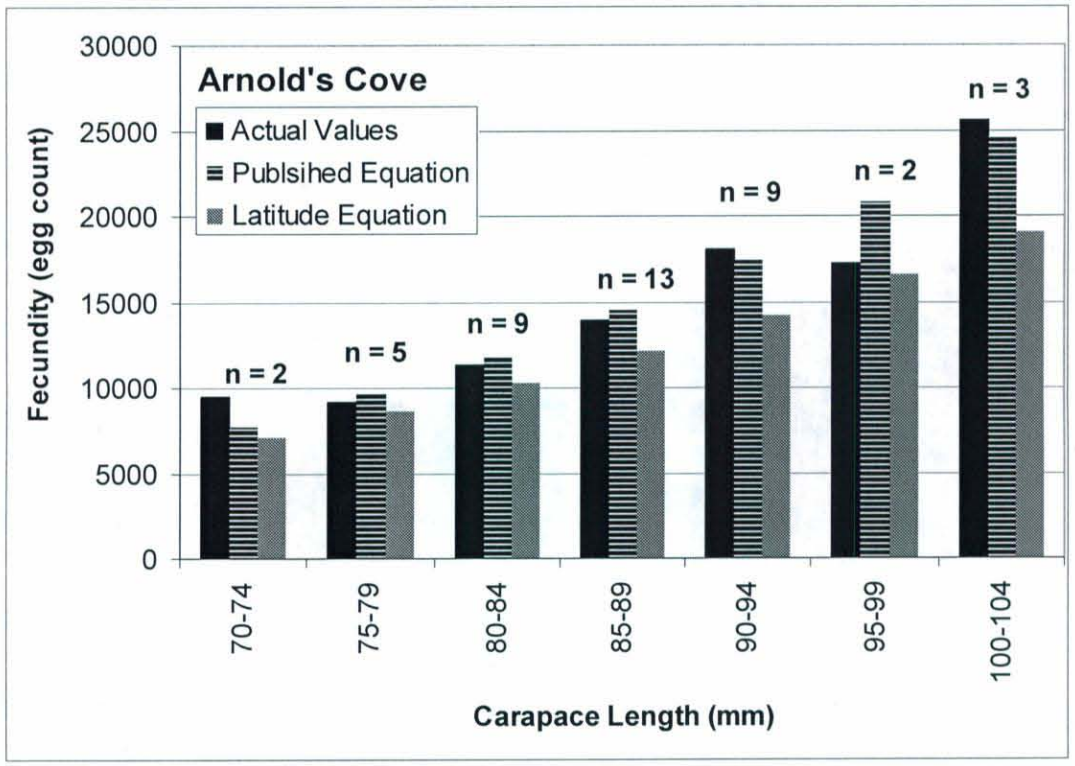
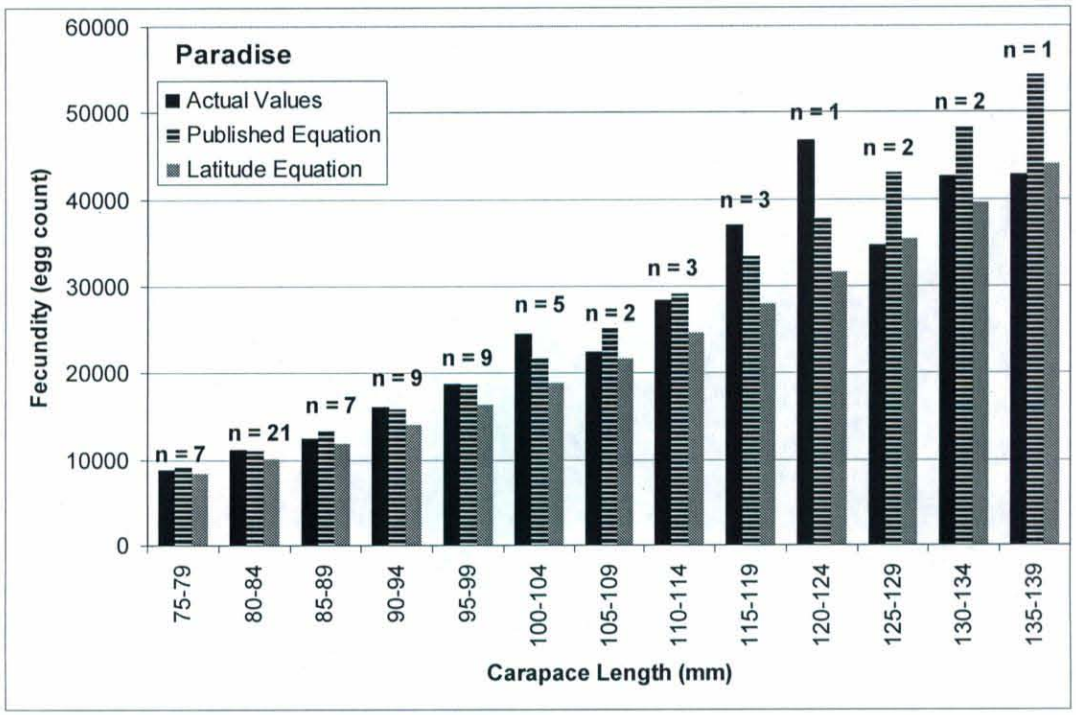
Appendix 1

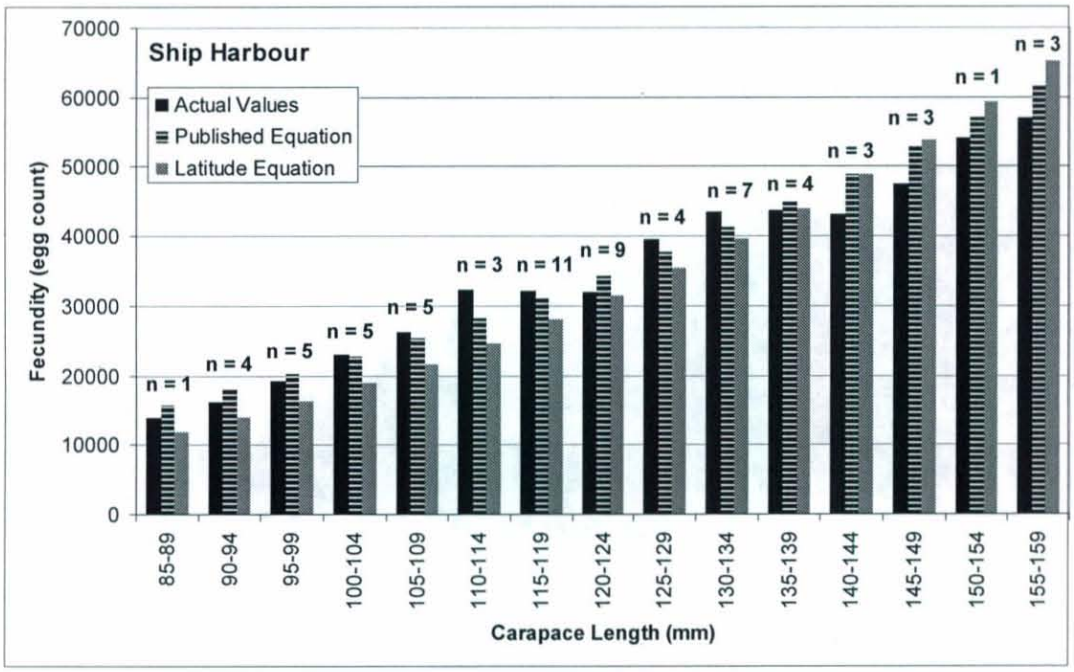
Difference in fecundity estimates made using the published fecundity equation and the Latitude Model # 2 equation to that of the observed/actual fecundity at various size classes.

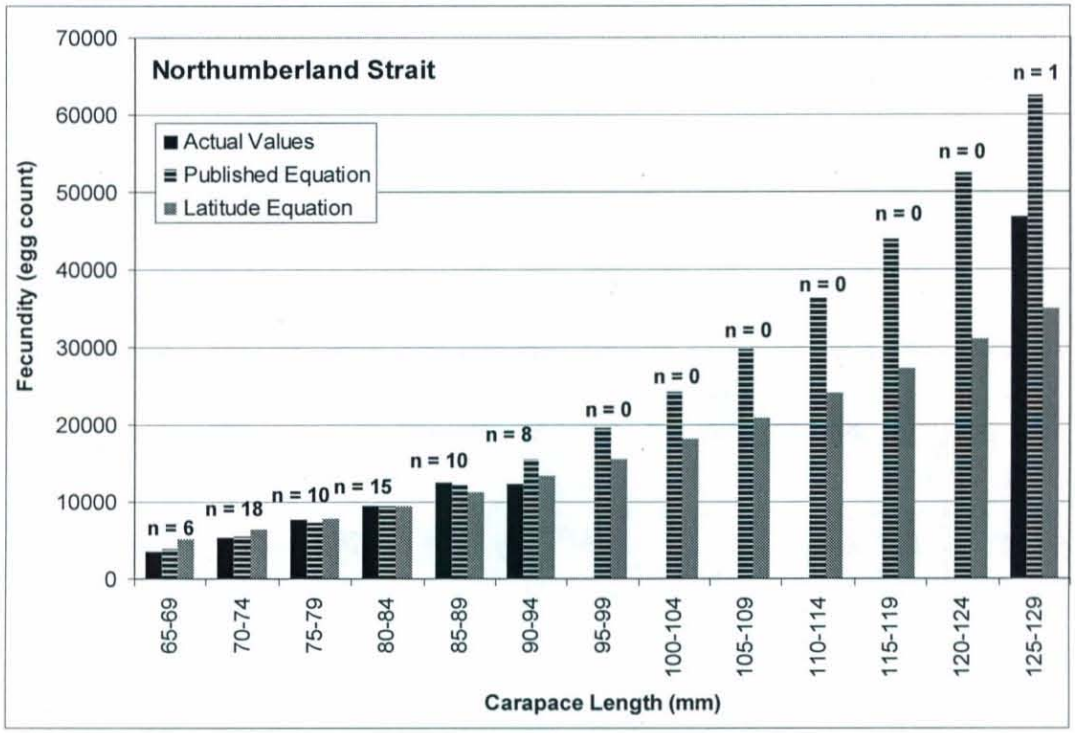


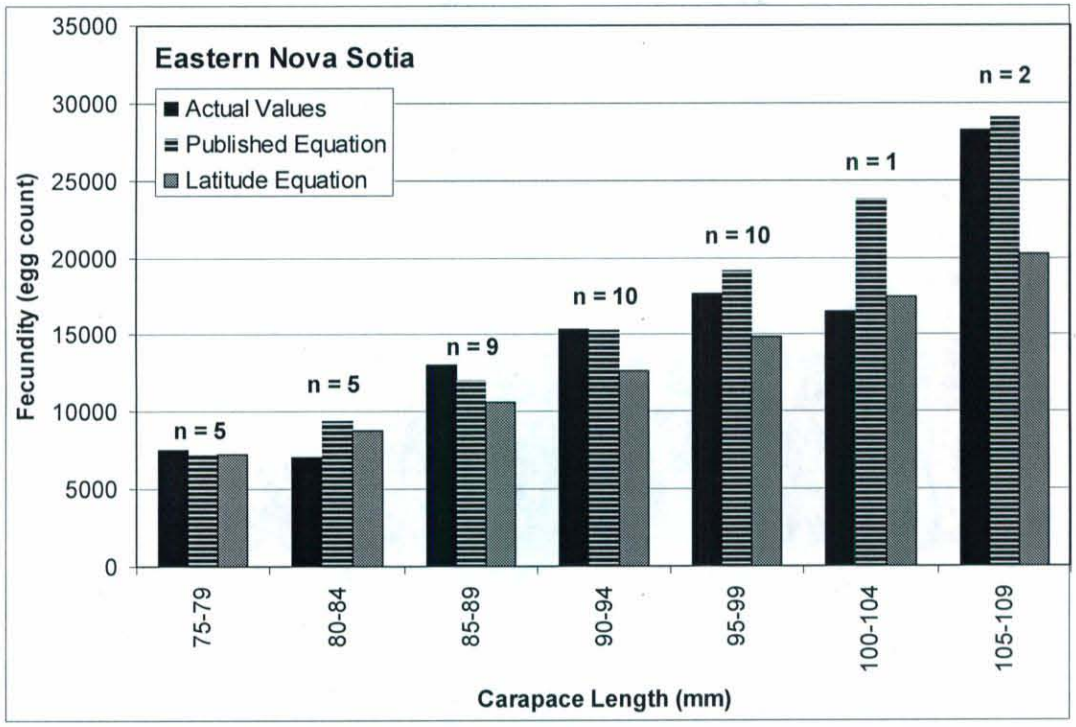


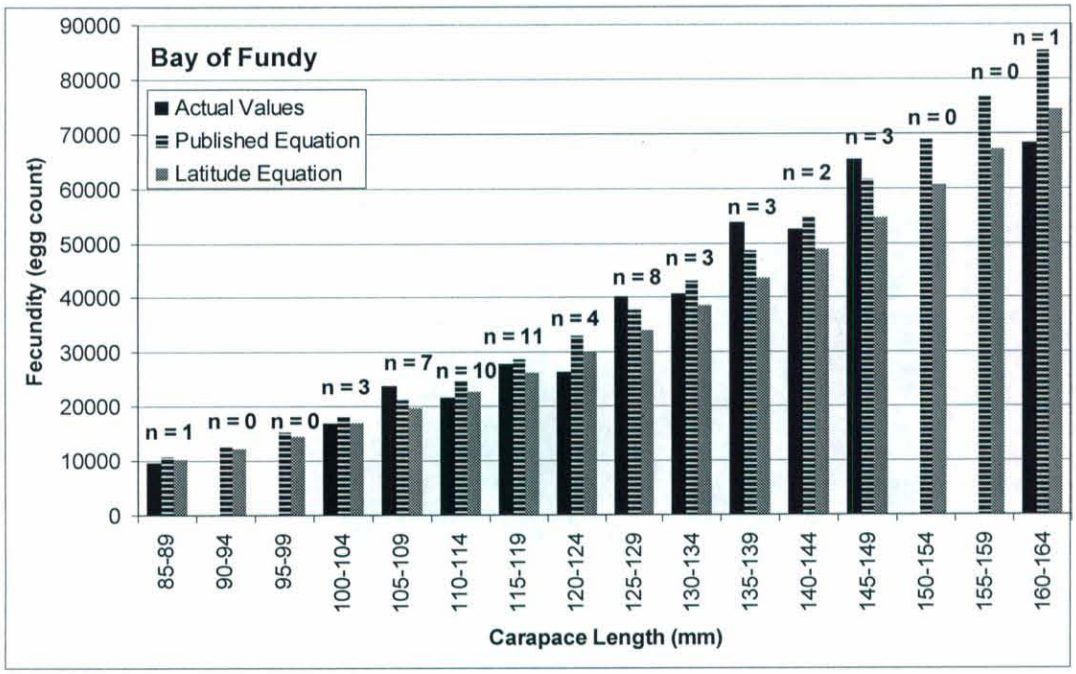

Arnold's Cove
Actual Values
Publsihed Equation
Latitude Equation
Fecundity (egg count)
30000
25000
20000
15000
10000
5000
0
n = 2
n = 5
n = 9
n = 13
n = 9
n = 2
n = 3
70-74
75-79
80-84
85-89
90-94
95-99
100-104
Carapace Length (mm)

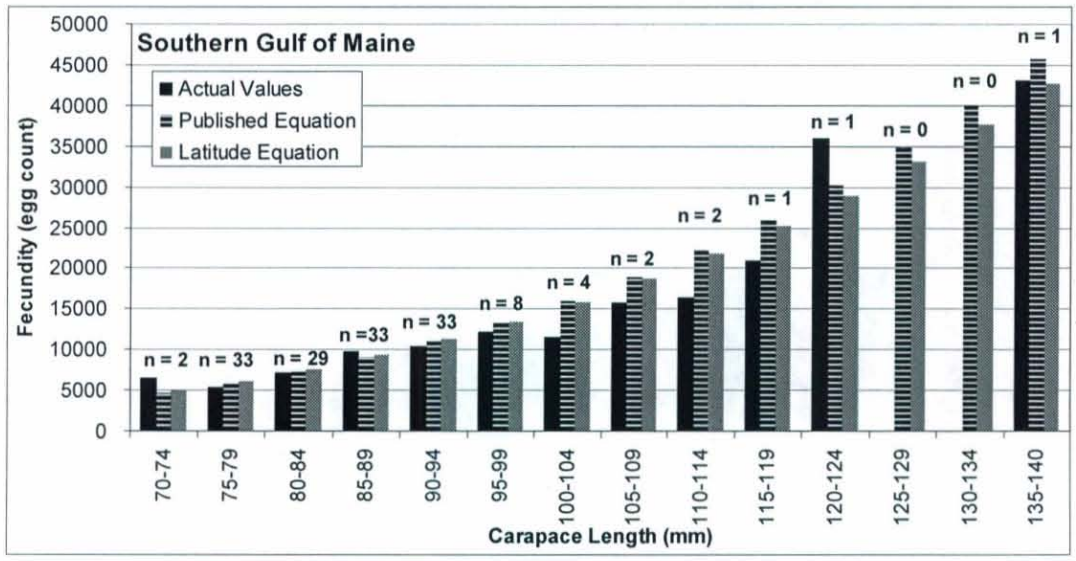

Paradise
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
60000
50000
40000
30000
20000
10000
0
n = 7
n = 21
n = 7
n = 9
n = 9
n = 5
n = 2
n = 3
n = 3
n = 1
n = 2
n = 2
n = 1
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
Carapace Length (mm)

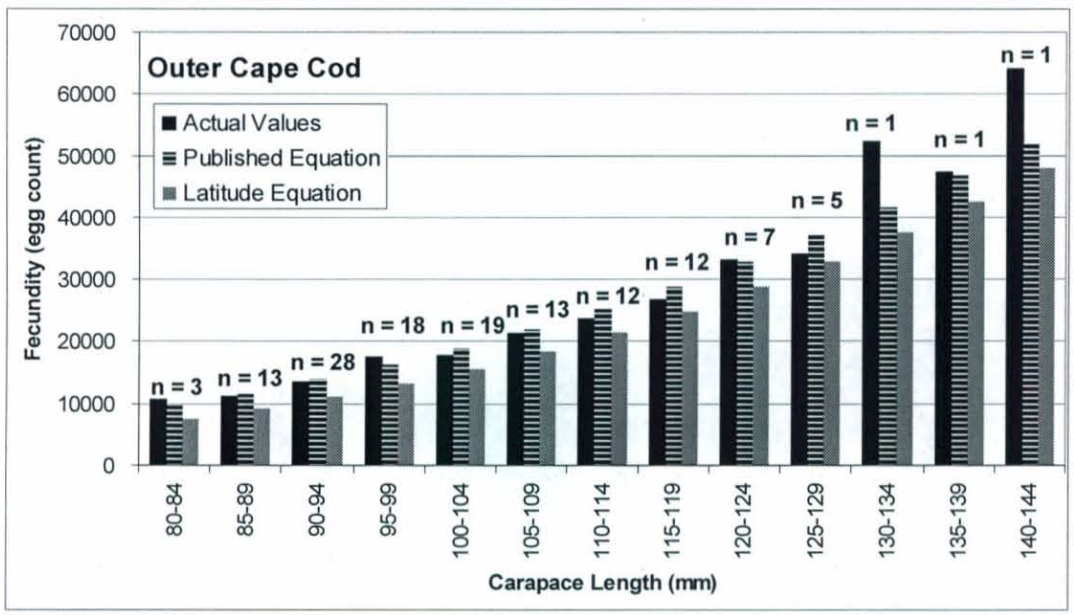

Ship Harbour
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
70000
60000
50000
40000
30000
20000
10000
0
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
n = 1
n = 4
n = 5
n = 5
n = 5
n = 3
n = 11
n = 9
n = 4
n = 7
n = 4
n = 3
n = 3
n = 1
n = 3

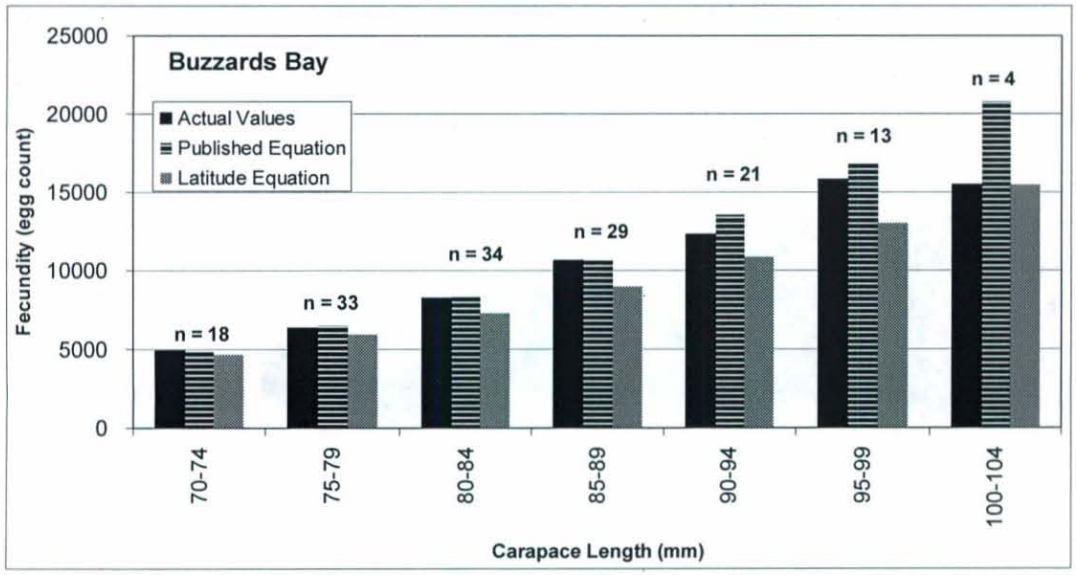

Northumberland Strait
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
70000
60000
50000
40000
30000
20000
10000
0
65-69
70-74
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
n = 6
n = 18
n = 10
n = 15
n = 10
n = 8
n = 0
n = 0
n = 0
n = 0
n = 0
n = 0
n = 1

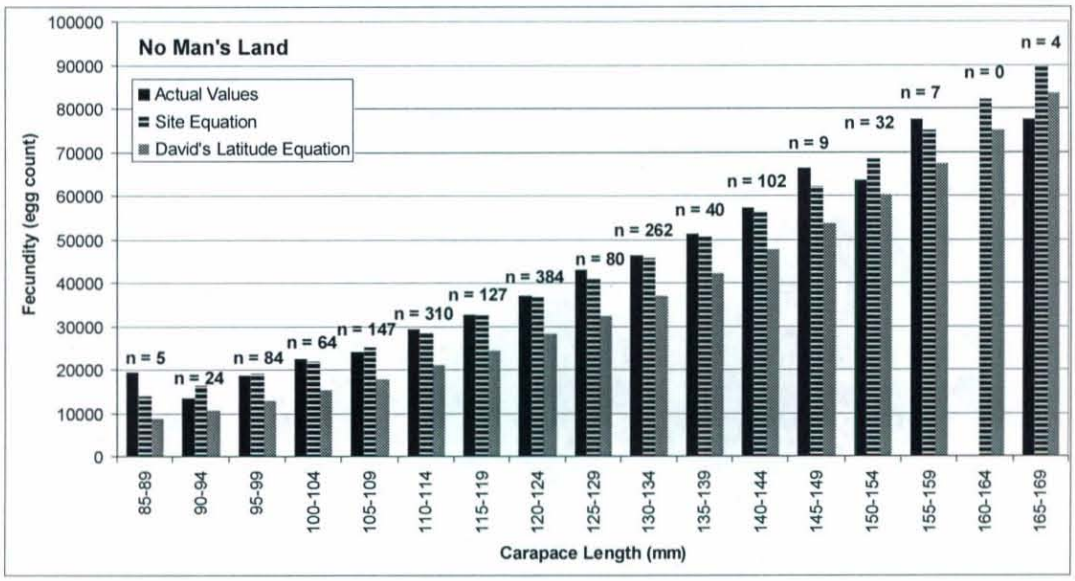

Eastern Nova Sotia
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
35000
30000
25000
20000
15000
10000
5000
0
75-79
80-84
85-89
90-94
95-99
100-104
105-109
n = 5
n = 5
n = 9
n = 10
n = 10
n = 1
n = 2


Bay of Fundy
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
160-164
n = 1
n = 0
n = 0
n = 3
n = 7
n = 10
n = 11
n = 4
n = 8
n = 3
n = 3
n = 2
n = 3
n = 0
n = 0
n = 1


Southern Gulf of Maine
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
n = 2
n = 33
n = 29
n =33
n = 33
n = 8
n = 4
n = 2
n = 2
n = 1
n = 1
n = 0
n = 0
n = 1
70-74
75-79
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-140

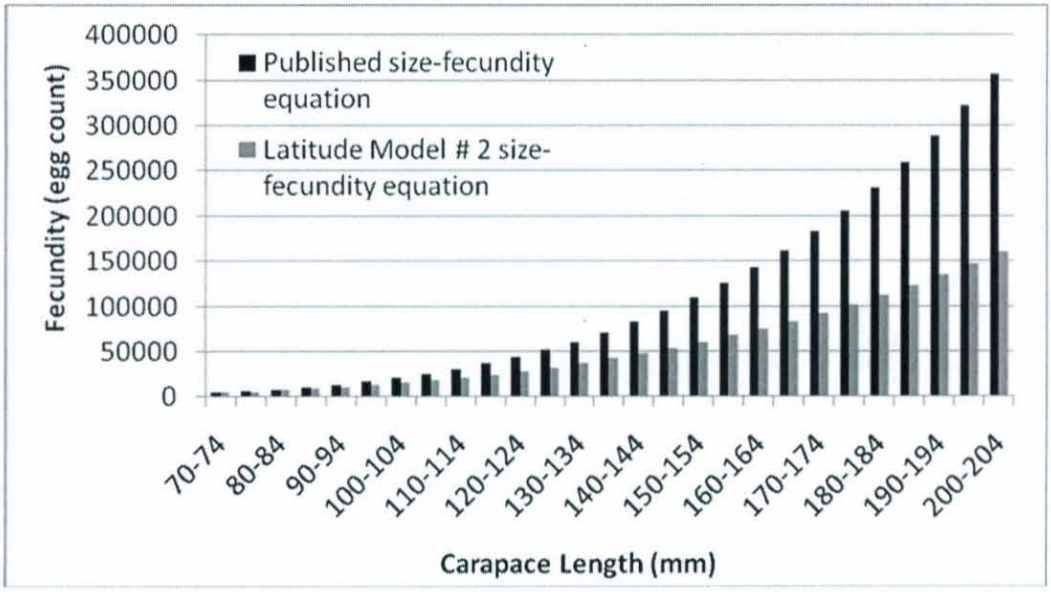

Outer Cape Cod
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
Carapace Length (mm)
n = 3
n = 13
n = 28
n = 18
n = 19
n = 13
n = 12
n = 12
n = 7
n = 5
n = 1
n = 1
n = 1
80-84
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144


Buzzards Bay
Actual Values
Published Equation
Latitude Equation
Fecundity (egg count)
25000
20000
15000
10000
5000
0
n = 18
n = 33
n = 34
n = 29
n = 21
n = 13
n = 4
70-74
75-79
80-84
85-89
90-94
95-99
100-104
Carapace Length (mm)


No Man's Land
Actual Values
Site Equation
David's Latitude Equation
Fecundity (egg count)
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
n = 5
n = 24
n = 84
n = 64
n = 147
n = 310
n = 127
n = 384
n = 80
n = 262
n = 40
n = 102
n = 9
n = 32
n = 7
n = 0
n = 4
85-89
90-94
95-99
100-104
105-109
110-114
115-119
120-124
125-129
130-134
135-139
140-144
145-149
150-154
155-159
160-164
165-169
Carapace Length (mm)

Appendix 2

Fecundity estimates for Buzzards Bay Massachusetts using the Buzzards Bay equation published in the literature and the equation generated for this site using the Latitude Model # 2, to show the over estimation, in fecundity estimates, for larger lobsters when using the published equation based on log-log transformations.



Appendix 3

R-Code for analysis:

```
> lobster<-read.csv(file="D:\\Desktop\\Rtest2loc.csv",head=TRUE,sep=",")
> library(nlme)
> lobster.m1<-nls(Fec~a*CL^b,data=lobster, start=list(a=0.001,b=3))
> summary(lobster.m1)
> lobster.m2<-nls(Fec~a[Loc]*CL^b[Loc],data=lobster, start=list(a=c(0.001,0.001,0.001),
b=c(3,3,3)))
> summary(lobster.m2)
> anova(lobster.m1,lobster.m2)
```